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TRAWLED CATCHES IN NORTHERN MORETON BAY
I. EFFECTS OF SAMPLING VARIABLES

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ABSTRACT

An analysis of variance approach was applied to catches of 60 species summed over 13 times, to evaluate the effects of sampling alternatives. These were: port and starboard nets, hauls with and into the tide, catches at midday and at dusk, and catches at three selected sites.

Use of Box and Cox transformations showed that each species required a different transformation to give a normal distribution.

Analyses were restricted to first order effects and second order interactions. In the former the heirarchy of importance of the sampling alternatives was sites >> time of day > port and starboard > tidal direction. In the latter the most important interaction was midday, dusk/the three sites. Various possible 'explanations' of interaction effects were attempted, but these were at best unconvincing. Most of the interactions appear to be due to random variations in the data.

INTRODUCTION

Enlargement of the Brisbane Airport has potential effects on a variety of marine biotas, and various 'before the event' studies have already been made, of which the most recent are Stephenson (1980a, b, c). Young and Wadley (1979) have also studied the catches of certain of the areas of interest using a small-mesh bream trawl, but no investigations had been made of the catches obtained by prawn trawlers using commercial nets. It was felt that of the possible effects of the constructional work at the Airport, those on the catches of prawn trawlers would be of the greatest economic significance, and for this reason the present investigation was commenced in early April 1979.

The immediate question is the acceptability of catches made by commercial prawn trawling gear. Jones (1973) was able to use catches from such gear effectively in his analyses of nekto-benthic invertebrates in Moreton Bay. More recently Stephenson and Burgess (1980) and Burgess (1980) have confirmed this. The present gear was identical with that used by Burgess (1980).

The present work involves analyses of the first year of data at three sampling sites: No. 1, Bramble Bay; No. 2, Redcliffe; and No. 3, S. of Middle Banks. Bramble Bay was chosen because it is adjacent to the Airport (ca 4 km), and may be affected by the partial filling of Serpentine Creek, and dredging of Jackson's Creek (see Fig. 1). The depth was ca 4 m and bottom primarily mud. Redcliffe is in the nature of a control site, distant from Airport activities; depth was ca 7 m and the bottom mud. The site south of the Middle Banks is south of the area from which sand fill for the Airport is to be obtained. Trawling could not be closer to the dredging site because the latter area is too confined for safe trawling. The site is in an area extensively used by commercial prawn trawlers; depth is ca 24 m and the bottom sandy mud.

Samples were collected at intervals of lunar months (28 days) beginning early April 1979 and extending for one year (13 months). At each site at each month three other sampling variables were involved: port and starboard nets, trawling with and against the tide, and sampling at midday and

dusk. Hence sampling involved 13 months × 3 sites × 2 times of day × 2 tidal directions × 2 nets, i.e. 312 samples in all. For each sample counts were made of the species collected, and for present purposes 60 species were considered. Of the five sampling variables, the main interest is in months and sites, and these (the 'prime variables') can be analysed using a sampling dimension of 13 months × 3 sites, with summing of catches over the other variables.
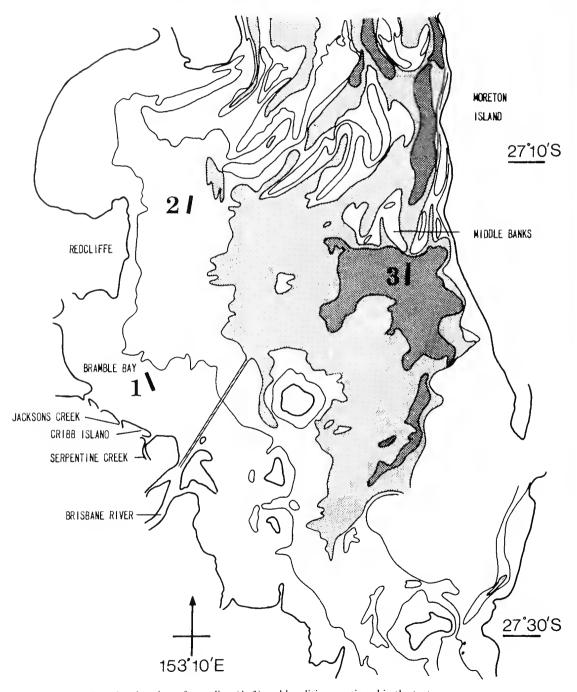

FIG. 1: Moreton Bay showing sites of sampling (1–3) and localities mentioned in the text.

Prior to so doing, it was thought to be of interest to evaluate the effects of the three remaining pairs of sampling variables (port/starboard nets, with/against tide, and midday/dusk). We can thus determine firstly whether port and starboard nets catches can be regarded as authentic replicates, as might be expected. Jones (1973) concluded that direction of trawling relative to the tide had very little effect on catches of nekto-benthic invertebrates, and the present more extensive data allows checking of his conclusions as well as extending them to the trawled fishes. While catches at midday and dusk are almost certainly different, quantification of results on the individual species is of interest from the light it throws on feeding habits and temporal 'niches'. Present analyses also cover one of the 'prime variables' — sites.

Catches at three sites are expected to be different and Stephenson and Burgess (1980) should be consulted for site patterns of species of fish in Moreton Bay. By using only three sites and establishing as we do, species which have significantly different site-distributions, we can reverse the approach of Stephenson and Burgess. The latter involved first establishing patterns by use of cluster analyses and then performing 'pseudo-*F*' tests on species recordings. (See Stephenson and Campbell 1977 for the 'pseudo-*F*' test). In the present case we use *F* tests first and then effect clustering using species with significantly different site-recordings.

SAMPLING PROCEDURES AND FORM OF THE DATA

Catches were of 15 min duration, including the time lowering and raising the net. It is appreciated that there will be some contamination of catches by midwater and surface water species, particularly at the deeper site 3, with shorter hauls this contamination would have been proportionally greater. With each haul catches from port and starboard nets were considered separately. One haul was made either into or with the tide and after ca 30 min a second was made in the reverse direction. At each site the procedure was repeated at midday and dusk, giving a total of 8 catches for each site at each time.

In each catch individuals of each well-known species were counted on board and not retained. All specimens of the less well-known species were preserved, identified at base and counted. Fish identifications were from Marshall (1964), Munro (1967), and Grant (1975) supplemented by invaluable assistance from Mrs. Deborah Burgess and Professor J.M. Thomson. Cephalopod identifications were made by Mrs. Pauline Dayaratne, Ministry of Fisheries, Colombo, Sri Lanka. Penaeid prawns were identified mainly from Dall (1957), alpheids from Banner and Smalley (1969), and the portunid crabs, other decapods and stomatopods by the senior author.

DATA REDUCTION

Study of sampling variables, including interaction effects, involves analysis of variance or related approaches and these become decreasingly satisfactory as species become increasingly absent from the samples, for example it is pointless to effect analyses on a species found in only 2/312 cases. Species were ranked by the number of samples of occurrence (ubiquity) and only the 60 species most frequently present of the total of 117 species were considered. Ubiquities ranged from 291 to 27.

The 60 species were then further rearranged to give an abundance hierarchy and allocated code numbers which are given in Appendix 1 together with their systematic names. Subsequent reference to a species is either by code number or by generic name — unless more than one species of a genus is listed.

SELECTION OF ANALYTICAL METHODS

The GLIM software computer package (Baker and Nelder 1978) was used to analyse the sets of data in the present study. Restrictions to the size of data blocks which can be analysed by GLIM on the University of Queensland PDP 10 computer precluded the use of the complete 5-way classification (312 values per species). Values were therefore summed over time (13 times) because this action produced the greatest data condensation; interactions of other sampling variables with time unfortunately were eliminated.

Preliminary analyses of data using GLIM showed that the data did not follow any of the common distributions. It was decided (a) to transform species data to obtain close approximations to normal distributions using Box and Cox transformations (see Appendix 2) and (b) to perform an analyses of variance on the transformed data for each species using GLIM. Models fitted included only first order effects and second order interactions.

TABLE 1: TRANSFORMATIONS AND FIRST AND SECOND ORDER EFFECTS.

Transformations			First order effects				2×2 Second order effects with probability		2×3 Second order effects with probability		
			P/S	W/I	M/D	S1,2,3	PS/MD	WI/MD	PS/S1,2,3	WI/S1,2,3	MD/S1,2,3
Species code no.	b	Std error b	Larger Prob.	Larger Prob.	Larger Prob.	Largest Prob.			Larger Largest Prob.	Larger Largest Prob.	Larger Largest Prob.
1	0·0752	0·136			M 0·5	2 0·1	1			1, 2 5	M, 1 0·1
2	−0·0688	0·184				2 0·1					
3	−0·227	0·563			M 0·5	3 0·1					D, 1 0·5
4	−0·572	0·339	S 2·5		M 5	3 0·1					
5	0·134	0·352				2 0·1					
6	0·461	0·284				2 0·1					D, 2 5
7	* 0·282	0·121	P 2·5		D 0·1	2 0·1					M, 1 0·1
8	0·486	0·628	P 1		D 0·1						
9	0·153	0·183	P 1		D 0·1						
10	−0·219	0·300	P 2·5		D 0·1	3 0·1					D, 1 0·1
11	0·0439	0·170		W 0·1		3 0·1					
12	0·167	0·136	P 2·5		D 0·5	3 0·1					
13	−0·289	0·287			D 0·5	2 0·1					
14	0·110	0·140	S 0·1		M 0·1	1 0·1		0·5			M, 2 2·5
15	−0·188	0·152	P 2·5	W 1		3 0·1					
16	* 0·816	0·245		W 5	D 0·1	1 0·5	5				M, 1 5
17	−0·379	0·161				1 0·1					
18	0·237	0·233				1 0·1					D, 2 0·5
19	0·155	0·312				3 0·5					
20	0·131	0·168			D 5	3 0·1					
21	*−0·449	0·177				3 0·1					
22	−0·343	0·509			D 0·1	3 2·5	5	1	S, 2 5	W, 1 5	
23	*−0·589	0·190	P 5			3 0·1	1		S, 1 2·5		M, 2 0·5
24	0·241	0·165			M 0·5	1 0·1					M, 1 2·5
25	0·112	0·157			D 0·1	2 0·5		5			
26	0·153	0·176			D 2·5	1 0·1					
27	−0·0563	0·172				3 0·1					
28	−0·123	0·179				3 0·1			P, 1 2·5	W, 2 5	
29	−0·143	0·249			D 0·5	3 0·1					
30	−0·0689	0·184		1 2·5		1 0·1	.				D, 1 0·1
31	−0·350	0·197			D 0·1	2 0·1					D, 1 0·1
32	0·153	0·198	P 2·5		D 2·5	3 0·1				1, 3 5	D, 1 2·5
33	−0·164	0·199				2 0·1					D, 1 0·5
34	−0·226	0·200	S 2·5			3 0·1	2·5		S, 2 0·5		
35	0·298	0·239				3 0·1					
36	−0·409	0·221				3 0·1					
37	0·0670	0·0451	P 2·5		D 2·5						
38	−0·205	0·241				1 0·5					
39	* 0·0745	0·00742						2·5			
40	−0·161	0·235	P 5	W 5		3 0·1			S, 2 1		
41	*−0·560	0·210				3 0·5		5			
42	−0·343	0·218			D 0·1	1 0·1					M, 1 2·5
43	−0·435	0·262			M 0·5	3 0·1					M, 2 0·5
44	*−1·135	0·297			D 1	3 0·1					
45	−0·512	0·252		I 0·5	M 0·1	1 0·1				I, 2 0·1	M, 2 0·1
46	0·172	0·245			D 5						D, 1 5
47	−0·143	0·261				3 0·1					
48	*−0·776	0·311				3 0·1					
49	0·0468	0·284									
50	−0·0832	0·271	P 1			3 0·5					

TABLE 1: (Continued)

Species code no.	b	Std error b	P/S Larger Prob.	W/I Larger Prob.	M D Larger Prob.	S1,2,3 Largest Prob.	PS/MD	WI/MD	PS/S1,2,3 Larger Largest Prob.	WI/S1,2,3 Larger Largest Prob.	MD/S1,2,3 Larger Largest Prob.
							2×2 Second order effects with probability		2×3 Second order effects with probability		
51	*−0·204	0·00251			D 0·1	1 0·1			S, 3 5	W, 3 5	D, 3 2·5
52	*−0·240	0·00292			D 5	1 0·1					D, 1 2·5
53	−0·184	0·287				1 1					
54	−0·464	0·309				3 0·1	5		P, 3 5		
55	*−0·438	0·00315			D 2·5	3 0·1					
56	*−0·547	0·00363				3 0·1					
57	*−0·459	0·00334		1 5	D 5	1 0·1					D, 1 0·5
58	*−0·371	0·00529				1 0·5	2·5	0·5	P, 3 2·5	W, 2 2·5	M, 2 5
59	*−0·523	0·00402			M 0·5	3 0·1					M, 3 0·5
60	*−0·524	0·00430	P 2·5			1 0·1					

Probabilities throughout as percentages.
Cols 2 and 3. Value of b used in transformation and standard error. Values of b significantly different from zero indicated by asterisk. Cols 3, 4, 5 and 6. Significant first order effects of port/starboard, with tide/into tide, midday/dusk, and sites 1, 2 and 3 respectively. The larger catches indicated by P or S, W or I, M or D, and 1, 2, or 3 respectively.
Cols 7 and 8. Significant second order effects involving 2x2 factors, with probabilities.
Cols 9, 10, and 11. Significant second order effects involving 2x3 factors. The larger 2 factor catch indicated by alphabetic abbreviation, and the largest 3 factor catch by the site number. Probabilities also given.

RESULTS (SEE TABLE 1)

TRANSFORMATIONS

The Box and Cox transformations (see Appendix 2) taking as a model

$$y^1 = \{(y+1)^b - 1\}/b$$

where y^1 is the transformed and y the original value, gave values of b and standard errors of b as shown in Table 1. The range in b values is from 0.816 (b not significantly different from 1) to an extremely stringent -1.135. It should be noted that only 16 of the b values are significantly different from zero, and for the remainder the log $(y+1)$ transformation would have been permissible.

FIRST ORDER EFFECTS

Only *significant* effects are considered.

PORT/STARBOARD NETS

Fifteen species gave significant results and of these 12 gave higher catches with the port net and three with the starboard. The twelve port species are all bottom-dwelling or near bottom-dwelling and comprise: *Metapenaeus bennettae, Portunus pelagicus, Penaeus plebejus, Sillago maculata, Portunus hastatoides, Callionymus limiceps, Metapenaeopsis, Centropogon, Sepia, Pseudorhombus arsius, Platycephalus* and *Phalangipus*. The three caught in significantly larger numbers by the starboard net are midwater or pelagic species and comprise *Loligo, Hyperlophus* and *Trachurus*.

WITH/INTO TIDES

Only seven species gave significant effects (of which three are at the 5% significance level), and overall this is the least important sampling variable at the first order level. Four species gave higher catches with the tide (*Saurida undosquamis, Callionymus limiceps, Thrissocles,* and *Pseudorhombus arsius*) and three were higher into the tide (*Sphyraena, Spheroides pleurostictus* and *Dorippe*).

MIDDAY/DUSK

Thirty species gave significant effects, with eight giving higher midday catches. Five of the eight are probably midwater species (viz. *Paramonacanthus, Apogon, Loligo, Hyperlophus* and *Harengula*). The 22 species with higher dusk catches contain five species of penaeid prawns (*Metapenaeus bennettae, M. endeavouri, Penaeus plebejus, P. esculentus,* and *Trachypenaeus*), three portunid crabs (*Portunus pelagicus, P. hastatoides* and *P. sanguinolentus*), two stomatopods (*Oratosquilla anomala,* and *Alima laevis*) and the crab *Dorippe*.

The remaining species occurring in greater numbers at dusk are primarily fish comprising *Sillago maculata, Pomatomus, Thrissocles, Apogonichthys, Johnius, Centropogon, Euristhmus, Spheroides hamiltoni, Priopidichthys* and *Suggrundus; Sepia* is also in this group.

It is of interest to note that in two pairs of fairly closely related taxa one occupies the 'daytime niche' and the other the 'dusk niche'. The species are *Spheroides pleurostictus* day and *S. hamiltoni* dusk, and *Odontodactylus* day and *Alima* night.

SITES

This is clearly the most important sampling variable at the first order level, with 55 species showing significant effects. The five species which failed to show effects are *Portunus pelagicus* (sp. 8), *Sepia* (sp. 37), *Scomberomorus* (sp. 39) *Spheroides hamiltoni* (sp. 46) and *Alpheus*

distinguendus (sp. 49). (Also four of these species failed to show second order interactions involving sites, the exception being *S. hamiltoni* with a midday-dusk/sites interaction at only 5% probability).

In Table 1 the sites with the largest mean (transformed) values are given and this shows 17 species with highest numbers at site 1, 9 at site 2 and 29 at site 3. Restricting consideration to these highest values can lead to a misleading grouping of species and a more representative picture is obtained by numerical classification. This was performed as follows: (a) using only the 55 species with significant site differences, (b) using mean transformed values of each species in each site, (c) standardising by totals to obtain proportionalities in each site and then (d) classifying species using Bray-Curtis dissimilarities and group-average sorting.
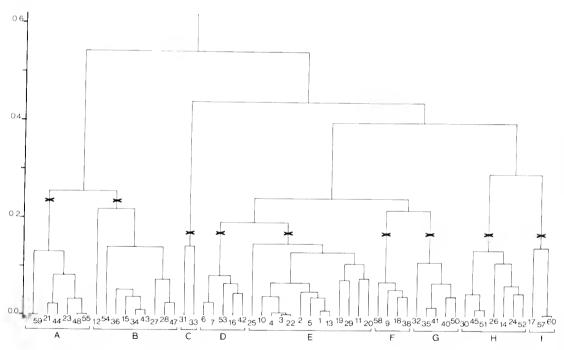
FIG. 2: Dendrogram showing classification of 55 species in the three sites. (For numbering of species see Appendix 1).

The species dendrogram which was obtained was interpreted at the nine group level, giving groups A–1, marked X in Fig. 2.

The proportional occurrences of species in the three sites were graded into H (high), M (medium) and L (low) and in Table 2 these grades in the nine species groups are given. This table shows that site 1 is characterised by high numbers

of the species in five species groups, site 2 by high numbers in two species groups (one very small), and site 3 by high numbers in three species groups. One of these last groups (species group A) contains a preponderance of rarer species. The largest species group (E) contains a preponderance of abundant species, and these occur in approximately coequal numbers in each site.

TABLE 2: TABULAR RESULTS OF CLASSIFICATION OF 55 SPECIES IN THREE SITES (SEE FIG. 2).

Species group	Species numbers from Appendix I	Graded Site 1	proportions Site 2	in sites Site 3
A	21, 23, 44, 48, 55, 56, 59	L	L	H
B	12, 15, 27, 28, 34, 36, 43, 47, 54	L	M	H
C	31, 33	L	H	L
D	6, 7, 16 42, 53	H	H	L
E	1, 2, 3, 4, 5, 10, 11, 13, 19, 20, 22, 25, 29	M	M	M
F	9, 18, 38, 58	H	L	M
G	32, 35, 40, 41, 50	H	L	H
H	14, 24, 26, 30, 45, 51, 52	H	M	L
I	17, 57, 60	H	L	L

Species in groups A–I rearranged by code numbers; proportionalities of occurrences in the sites graded into H—high, M—medium and L—low.

SECOND ORDER EFFECTS INTERACTIONS

Only significant effects are considered. For convenience these are divided into 2 factor × 2 factor and 2 factor × 3 factor groups, the three factors being the sites. To assist interpretation, the linear interaction components of each cell in the respective 2 × 2 and 2 × 3 tables were obtained.

2 × 2 INTERACTIONS

All cells in a 2 × 2 linear interaction table have identical absolute values, and conceptual interpretations are necessarily restricted. The three 2 × 2 interactions are:

(a) Port, starboard/with and against tide: no species involved (Hence not listed in Table 1).

(b) Port, starboard/midday, dusk: five species of which two are at the 5% probability level.

(c) With and against tides/midday, dusk: eight species, three at the 5% level.

Overall the 2 × 2 interactions appear relatively unimportant.

2 × 3 INTERACTIONS

From the linear interactions components one can select in each case the site giving the greatest interaction and which alternative state of the other factor is giving the higher catches. These are given in Table 1. The three 2 × 3 interactions are:

(a) Port, starboard/sites: eight species, three at the 5% level. Three with unusual catches at site 1, four at site 2 and one at site 3; three species with high catches in the port, and five in the starboard net.

(b) With and against tide/sites: seven species, four at the 5% level. Two with unusual catches at site 1, four at site 2, and one at site 3; five species with high catches with the tide, and two against the tide.

(c) Midday, dusk/sites: 22 species, only four at the 5% level. Fourteen with unusual catches at site 1, seven at site 2 and one at site 3; eleven species with high catches at midday and eleven at dusk.

DISCUSSION

Data on 60 species were summed over 13 times of sampling (1 year) and the effects of four remaining sampling variables were considered. The data were transformed to approximate normality using Box and Cox transformations and the range of power transformations required confirms the fact that the raw data did not conform to any standard distribution. One suspects that this applies generally to much marine data, and the choice of a single transformation (typically log $(y + 1)$) prior to analyses of such data appears objectionable.

First order effects of the four sampling variables showed that the number of species with significant differences was least when considering the with tide/against tide alternative (7 spp.). While possibly surprising, this result confirms Jones (1973) conclusions from work in Moreton Bay on nekto-benthic invertebrates. One third (21 out of 60) of the total number of species considered are relatively slow-swimming or non-swimming crustaceans which might be expected to occur more frequently in the with tide catches; there were no crustaceans amongst the seven species — all were fish. Also possibly surprising is the fact that species caught in significantly higher numbers in the two directions show no obvious relationships to modes of life. Rapidly swimming midwater fish (*Thrissocles* and *Sphyraena*) occur in each group. It seems likely that the with/against effects are due to random fluctuations in the data.

First order effects of port and starboard nets have already been briefly discussed. Fifteen species show significant effects and of these the three caught in significantly larger numbers in the starboard net are midwater species and the remaining twelve are bottom dwelling-species. There are various possible explanations for this difference, for example different net settings or different effects of propeller swirl. These are discussed further under port/starboard interactions with other variables.

Midday/dusk catches show important first order effects, with 30 species showing significant differences, eight giving higher midday catches and 22 higher dusk catches. Explanation of midday/dusk differences are offered in two main

directions, net avoidance and vertical movements of the species. At midday because of greater visibility, one might expect increased net avoidance, particularly by the more mobile species. In fact, of the eight species caught preferentially at midday, five are highly mobile (*Paramonacanthus, Apogon, Hyperlophus, Harengula* and *Loligo*). The five are probably primarily midwater species, and possibly the higher midday catches are due, fundamentally, to downwards movement during the daytime. It should be noted that three of the above species (*Paramonacanthus, Apogon* and *Loligo*), are amongst the four most abundant of the species in the catches and comprise 57% of the total catches.

The 22 species showing higher dusk catches contain eleven species of crustaceans. It is likely that these are buried by day and move above the substratum at dusk. The significantly higher dusk catches of five of the six species of penaeid prawns were to be expected since it is known that the Moreton Bay prawn fishery is mostly conducted from dusk to dawn. Nine of the species with higher dusk catches are fish, which presumably occur in high numbers in the water column during the day (the tenth fish *Suggrundus* is an exception). Possibly their concentration near the bottom at night is primarily to feed on nekto-benthic forms which have emerged from the substratum.

First order effects of sites show that this is the most important sampling variable, with significant differences in site catches in 55 out of the 60 species. We classified the data on the significant species in sites, thus reversing the usual procedures in which classification preceeds tests of conformity. The results (see Table 2) have already been discussed briefly. Seventeen species occur in groups with lowest numbers at site 3 and 16 species in groups with highest numbers at site 3.

Interpretation of second order effects presents difficulties, particularly those involving 2 factor/2 factor interactions and these are now discussed. We first consider the possibility that the differences between port and starboard nets is due to the latter 'riding' somewhat higher. If so fishing into the tide should change the port/starboard differential, and lead to a noticeable port, starboard/with, against the tide interaction effect. In fact no species show significant interactions of this type. Assuming that at dusk several species of crustaceans move from the substratum into the water column, these should appear in larger numbers in the starboard net at dusk and lead to noticeable interaction involving port and

starboard/midday and dusk. In fact only five species show significant interactions.

We next consider 2 × 2 factor interactions involving midday and dusk. Visual stimuli for net avoidance will be stronger at midday than at dusk and this should result in differential effects with and against the tide (because hauls with the tide move faster over the bottom). Only eight species show significant with and against the tide/midday and dusk interactions and they include both highly mobile fishes *(Hyperlophus* and *Scomberomorus)* and relatively slow moving crustaceans *(Penaeus esculentus, Trachypenaeus, Oratosquilla woodmasoni* and *Thenus).*

We now consider 2 factor/3 sites interaction. The data shows that one species (52) is restricted to site 1, and four (44, 50, 51 and 54) are restricted to site 3. With such species the 2 factor recordings in the vacant sites are equal and interaction effects will necessarily be due to the occupied site. Of the total of thirty-seven 2 factor/3 site interactions five are accounted for in this way — three for species 51, one for species 52 and one for species 54. This leaves thirty-two 2 factor/3 factor interactions for consideration.

Of these six species show significant port, starboard/3 sites interactions. While intrinsically unlikely because of the lengths of the trawl warps, it is possible that part of the first order port/starboard effect is due to propellor swirl. If so there should be similar effects at the shallower sites 1 and 2, and interactions should be concentrated at site 3. In fact interactions are greatest at sites 1 and 2 in five of the six species which are involved.

Of the 32 interactions discussed above, only three involve with and into tides and sites. No rational explanation could be found for first order with/into effects, and it appears even more likely that interaction effects are due to randomness in the data.

Of the 29 significant midday, dusk/3 sites interactions, 11 involve higher midday catches and nine higher dusk catches. The ratio 11:9 is markedly different from the 8:22 ratio of midday/dusk species at the first order level. Restating the situation, the problem is why relatively few of the benthic, near benthic and benthic feeding species occur in significantly higher numbers at dusk in the shallower sites 1 and 2. No explanation can be offered.

Significant interactions are unevenly distributed among species, with over half the species (32 out of 60) giving no significant interaction, and four species *(Paramonacanthus, Penaeus esculentus,*

Metapenaeopsis and *Thenus)* giving 15. A third of the interactions is due to these four species.

In summary, attempts have been made to explain interactions in meaningful terms instead of invoking random variation, but in general these explanations appear invalid or at best unconvincing. In conjunction with the concentration of interactions within a few species, one must conclude that the vast bulk of the interactions are due to random events.

One of the important objectives of the present analyses was to determine which sampling variables could be regarded as replicates for the purposes of further times series analyses. Data from only two species (spp. 39, 49) can be so regarded over all sampling variables. Working on within-sites data another 18 species can be regarded as replicates over the three remaining sampling variables. Accepting that differences between with and into the tide samples are due to random variations, two further species (spp. 11, 30) can be added. For the remaining species summing recordings within sites will involve additions of values which are significantly different. The greatest differences will be between midday and dusk values and there are two practicable alternatives for later analyses: six analyses with midday and dusk/site combinations or three analyses each involving midday and dusk summations. The latter was chosen because division of catches into two components generally leads to improverished data in each. This would be especially disadvantageous in the case of the 30 species for which significant differences between midday and dusk catches have not been demonstrated.

ACKNOWLEDGEMENTS

APPENDIX 1

SPECIES CONSIDERED

CODE NO.	SPECIFIC NAME	SYSTEMATIC POSITION	NO. OF INDIVS	NO. OF CATCHES
1	*Paramonacanthus oblongus* (Temminck & Schlegel)	Monacanthidae, Pisces	44975	195
2	*Leiognathus moretoniensis* Ogilby	Leiognathidae, Pisces	18528	215

	Species	Family		
3	*Apogon quadrifasciatus* Cuvier & Valenciennes	Apogonidae, Pisces	9737	290
4	*Loligo formosana* Sasaki	Cephalopoda, Mollusca	8109	291
5	*Charybdis callianassa* (Herbst)	Portunidae, Crustacea	5207	194
6	*Polynemus multiradiatus* (Günther)	Polynemidae, Pisces	4718	213
7	*Metapenaeus bennettae* Racek & Dall	Penaeidae, Crustacea	4276	165
8	*Portunus pelagicus* (Linnaeus)	Portunidae, Crustacea	3253	279
9	*Penaeus plebejus* Hess	Penaeidae, Crustacea	2045	178
10	*Sillago maculata* (Quoy & Gaimard)	Sillaginidae, Pisces	1895	219
11	*Saurida undosquamis* (Richardson)	Synodontidae, Pisces	1559	141
12	*Portunus hastatoides* Fabricius	Portunidae, Crustacea	1247	138
13	*Pomatomus saltatrix* (Linnaeus)	Pomatomidae, Pisces	1086	159
14	*Hyperlophus translucidus* McCulloch	Clupeidae, Pisces	747	94
15	*Callionymus limiceps* Ogilby	Callionymidae, Pisces	725	110
16	*Thrissocles hamiltoni* (Gray)	Clupeidae, Pisces	636	85
17	*Pelates quadrilineatus* (Bloch)	Theraponidae, Pisces	608	66
18	*Gerres ovatus* Günther	Gerridae, Pisces	572	96
19	*Caranx malam* (Bleeker)	Carangidae, Pisces	560	90
20	*Apogonichthys ellioti* (Day)	Apogonidae, Pisces	544	116
21	*Callionymus belcheri* Richardson	Callionymidae, Pisces	520	61
22	*Penaeus esculentus* Haswell	Penaeidae, Crustacea	470	170
23	*Metapenaeopsis novaeguinae* (Haswell)	Penaeidae, Crustacea	445	58
24	*Harengula castelnaui* (Ogilby)	Clupeidae, Pisces	440	49
25	*Trachypenaeus fulvus* Dall	Penaeidae, Crustacea	438	93
26	*Johnius australis* (Günther)	Sciaenidae, Pisces	392	63
27	*Saurida tumbil* (Bloch)	Synodontidae, Pisces	381	76
28	*Priacanthus macracanthus* Cuvier	Priacanthidae, Pisces	323	82
29	*Oratosquilla anomala* (Tweedie)	Stomatopoda, Crustacea	307	104
30	*Sphyraena obtusata* Cuvier & Valenciennes	Sphyraenidae, Pisces	281	57
31	*Portunus sanguinolentus* (Herbst)	Portunidae, Crustacea	272	40
32	*Centropogon marmoratus* (Günther)	Scorpaenidae, Pisces	254	82
33	*Alpheus stephensoni* Banner & Smalley	Alpheidae, Crustacea	229	28
34	*Trachurus mccullochi* Nichols	Carangidae, Pisces	227	43
35	*Selaroides leptolepis* (Cuvier)	Carangidae, Pisces	221	70
36	*Charybdis truncata* Fabricius	Portunidae, Crustacea	172	60
37	*Sepia aculeata* Orbigny	Cephalopoda, Mollusca	131	80
38	*Thalamita sima* H. Milne-Edwards	Portunidae, Crustacea	129	63
39	*Scomberomorus queenslandicus* Munro	Scombridae, Pisces	122	59
40	*Pseudorhombus arsius* (Hamilton & Buchanan)	Bothidae, Pisces	110	60
41	*Upeneus tragula* (Richardson)	Mullidae, Pisces	110	54
42	*Euristhmus lepturus* (Günther)	Plotosidae, Pisces	101	57
43	*Pseudorhombus* spp. (juveniles)	Bothidae, Pisces	99	50
44	*Metapenaeus endeavouri* (Schmitt)	Penaeidae, Crustacea	92	31
45	*Spheroides pleurostictus* (Günther)	Tetradontidae, Pisces	92	53
46	*S. hamiltoni* (Gray & Richardson)	Tetradontidae, Pisces	87	58
47	*Oratosquilla interrupta* (Kemp)	Stomatopoda, Crustacea	84	55
48	*Octopus membranaceus* Quoy & Gaimard	Cephalopoda, Mollusca	77	47
49	*Alpheus distinguendus* de Man	Alpheidae, Crustacea	76	37
50	*Platycephalus indicus* (Linnaeus)	Platycephalidae, Pisces	74	53
51	*Priopidichthys marianus* (Günther)	Centropomidae, Pisces	74	27
52	*Alima laevis* (Hess)	Stomatopoda, Crustacea	70	41
53	*Siganus spinus* (Linnaeus)	Siganidae, Pisces	60	38
54	*Oratosquilla woodmasoni* (Kemp)	Stomatopoda, Crustacea	58	39
55	*Suggrundus harrisii* (McCulloch)	Platycephalidae, Pisces	52	33
56	*Minous versicolor* (Ogilby)	Scorpaenidae, Pisces	48	29
57	*Dorippe australiensis* Miers	Dorippidae, Crustacea	46	29

58	*Thenus orientalis* (Lund)	Scyllaridae,		
		Crustacea	43	27
59	*Odontodactylus cultrifer*	Stomatopoda,		
	(White)	Crustacea	39	27
60	*Phalangipus*	Majidae,		
	australiensis Rathbun	Crustacea	38	27

APPENDIX 2
THE BOX-COX TRANSFORMATION

The Box-Cox transformations (Box & Cox 1964) constitute a family of transformations (including logarithms) of a dependent variable, instituted to obtain a transformation that most nearly satisfies the classical assumptions of least squares analyses of data. These assumptions are: (A) that the expected value of the dependent variable y should be a linear function of a set of p independent variables $x_1, \ldots, x_p$ and (B) that the errors are additive with constant variance. Hence, writing η for an error,

$$y = \beta_o + \sum_{j=1}^{p} \times_j \beta_j + \eta$$

Here the β_j's are regression coefficients scaling the effect of the x_j's on the dependent variable y and β_o is the mean value of y at zero values of the independent variables.

By an appropriate choice of the x_j's this formulation includes the models for regression, the analysis of variance and convariance, factorial designs etc. However, it is often preferable to look for transformations $y^1 = f(y)$ such that

$$y^1 = \gamma_o + \sum_{j=1}^{p} \times_j \gamma_j + \varepsilon \ldots \ldots (1)$$

where the errors ε satisfy assumption (B) and the y_j's are regression coefficients. So in our choice of y^1 we attempt to find a scale on which y^1 satisfies conditions (A) and (B). In practice, the most useful transformations are powers and logarithms, often translated by a constant. The Box-Cox family of transformations is:

$$y^1 = (y+a)^b - 1 / b \text{, if } b \neq 0$$

or

$$y^1 = ln (y+a) \text{, if } b = 0$$

The use of y^1 rather than $(y+a)^b$ (for $b \neq 0$) ensures that the transformation $y^1 = ln (y+a)$ gets smoothly into the family as b passes through zero. Box and Cox originally fixed a at zero and estimated b from data at hand. In the present case a was fixed at 1 to avoid logarithms of zero (corresponding to zero counts) in the classical manner. The alternative possibility of estimating both a and b from the data complicates the analysis and was found in trial analyses on the present data to produce computational instability. This supports a sensible fixed choice of a. The value of b is found by maximum likelihood estimation. There are two principle approaches to this: first is the original method of Box and Cox and fits model (1) for a given b, adjusts b and repeats the procedure. Essentially, the value of b leading to the smallest sum of squared errors provides our estimate. The second is to use a numerical function maximisation routine based on the likelihood of the data and its first and second derivatives. We followed the second approach, utilising the Numerical Algorithms Group (1978) Library routine E04LBF. The source for an interactive FORTRAN program is available from the second author.

LITERATURE CITED

BAKER, R.J. and J.A., NELDER, 1978. 'The GLIM System: Release 3: Generalised Linear Interactive Modelling'. Part 2, Sections 7-20, (Numerical Algorithms Group: Oxford). p. 73.

BANNER, D.M. and C.R. SMALLEY, 1969. Contributions to the knowledge of the alpheid shrimp of the Pacific Ocean. Part XIII. *Proc. Roy. Soc. Qd* **81**: 43-50.

BOX, G.E.P. and D.R. COX, 1964. An analysis of transformations. *J. Roy Statist. Soc.* B. **26**: 211-52.

BURGESS, D.A., 1980. 'Numerical Analyses of Demersal Fish Assemblages in Northern Moreton Bay, Queensland'. Unpublished M.Sc. Thesis, Zoology Department, University of Queensland.

DALL, W., 1957. A revision of the Australian species of Penaeinae (Crustacea: Decapods: Penaeidae). *Aust. J. mar. Freshw. Res.* **8**: 136-230

GRANT, E.M., 1975. 'Guide to Fishes' (Co-ordinator-Generals Department: Brisbane), p.640.

JONES, A.R., 1973. 'The Structure of an Association of Nektobenthic Invertebrates from Moreton Bay'. Unpublished Ph.D. Thesis, Zoology Department, University of Queensland.

MARSHALL, T.C., 1964. 'Fishes of the Great Barrier Reef and Coastal Waters of Australia'. (Sydney: Angus and Robertson). p.566.

MUNRO, I.F.R., 1967. 'The Fishes of New Guinea'. (Port Moresby: Port Moresby Dept. of Agriculture, Stock and Fisheries). p.650.

NUMERICAL ALGORITHMS GROUP, NAG, 1978. FORTRAN Library Mini Manual, Mark 7, Vol. 4, Section EO4, (Oxford: Numerical Algorithms Group). 1-28.

STEPHENSON, W., 1980a. Flux in the sublittoral macrobenthos of Moreton Bay. *Aust. J. Ecol.* **5**: 95-116.
    1980b. Relationships of the macrobenthos of Moreton Bay to prawns and to abiotic factors. *Aust. J. Ecol.* **5**: 143-9.

1980c. Time patterns of macrobenthic species in Moreton Bay. *Aust. J. Ecol.* **5**: 245-62.

and D.A., BURGESS, 1980. Skewness of data in the analyses of species-in-sites-in-times. *Proc. Roy. Soc. Qd* **91**: 37-2.

and B.M. CAMPBELL, 1977. The macrobenthos of Serpentine Creek. *Mem. Qd Mus.* **18**: 75-94.

YOUNG, P.C. and V.A. WADLEY, 1979. Distribution of shallow water epibenthic macrofauna in Moreton Bay, Queensland, Australia. *Mar. Biol.* **53**: 83-97.

TRAWLED CATCHES IN NORTHERN MORETON BAY
II. CHANGES OVER TWO YEARS

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ABSTRACT

The trawled biota was sampled at monthly intervals for two years at three selected sites in northern Moreton Bay. This was part of a series of baseline studies of possible effects of enlarging the Brisbane Airport.

Most of the species-in-sites showed significant annual cycles, these being most developed at the site furthest from the mainland; other intersite differences are detailed.

A majority of the species-in-sites showed significant reductions in catches in the second compared with the first year of sampling, and annual cycling was also less developed in the second year. Residuals from annual cyclical regressions were examined by further regressions and in numerous species-in-sites there were significant linear reductions in catches. Ten-year cyclical regressions, which probably mimic long-term logistic declines, gave significant results in a majority of cases.

The major changes in the biota from year 1 to year 2 are probably related to a long period of warm and dry conditions during year 2. A very prolonged study would have been necessary before the effects of weather could have been quantified, and a basis found for assessing potential changes due to man.

Analyses were also conducted on data summed over the three sites. A higher proportion of species now showed significant annual cycling, and of these fewest attained their estimated times of maxima in spring, and most in summer. Comparing with previous results on the macrobenthos (Stephenson 1980c) supports the hypothesis that the benthos is largely controlled by nekto-benthos and nekton.

Comments are given on the total numbers of individuals of species in the combined catches at the three sites in terms of both faunistic recordings and numerical importance from a commercial viewpoint.

INTRODUCTION

In an early paper (Stephenson, Chant and Cook 1982) we have given the background to the present work. It is an attempted baseline study whereby the effects of enlargement of the Brisbane Airport upon the trawled biota may be evaluated. The study began in April 1979 and involved sampling at three sites for 26 lunar months (2 years). By this time engineering operations at the airport were about to commence, and results are reviewed primarily to assess the adequacy of a two year baseline study.

Descriptions of the three sites and a map were given previously; site 1 in Bramble Bay is close to the airport itself, site 2 near Redcliffe is in the nature of a control site, and site 3 near Middle Banks is close to the area of dredging fill for the airport.

At each site in each month, eight catches were made using three sampling alternatives: four catches involved port nets and four starboard, four with the tide and four into it, and four at midday and four at dusk. In the previous paper after an analysis of variance approach it was decided to sum catches of each species over these three alternatives. For present purposes the species considered at a given site were those in which more than 10 individuals were obtained and which occurred in more than two of the 26 times.

The 70 species which are considered are listed in alphabetical order in Appendix 1. Subsequent references are to generic names unless more than one species of a genus is listed in Appendix 1.

CYCLICAL REGRESSIONS

After attempting a variety of analytical approaches the use of cyclical regressions appeared the most promising. They have produced conceptual sense from benthic data in northern Moreton Bay (Stephenson 1978, 1980a, b, c), but Burgess (1980) using the same techniques obtained significant cycles in only 15/61 trawled fish species over 17 times (over two years).

DATA TRANSFORMATIONS

Prior to effecting cyclical regressions, the data were transformed so that the distributions approximated to a symmetrical bell-shaped curve. This was obtained by operating on the skewness of the data. A similar approach was used previously by the senior author (Stephenson and Burgess, 1980). Moment coefficients of skewness were obtained from the recordings of each species in the different times with a series of root transformations from 1 to 8 incremented by unity (i.e. $n^{1/1}$ to $n^{1/8}$). Two options are then available either to select the transformation which approximates most closely to completely removing skewness from the data (moment coefficient of zero) or to retain some of the original skewness (moment of 0·5). A trial of the two alternatives was made using summed data from the three sites and showed that with ca zero moment coefficients the R^2 value for annual cyclical regressions averaged over all species increased by less than 1% over that when using an 0·5 moment. It was decided to use moment coefficients of 0·5; this level was chosen because it may be used as a limit for normality of distribution prior to statistical testing. Thus Pearson and Hartley (1966) quote 5% points for the distribution of moment coefficients of skewness for samples which deviate significantly from a normal distribution. For less than 50 samples, the moments are always greater than 0·53.

In some species 8th root transformations did not reduce the moments to 0·5 and in these cases the 8th root was used.

Annual cyclical regressions (periodicity of 13 time units) were carried out on site 1 data for 49 species, appropriately transformed. The values of R^2 (proportion of explained variation) are readily tested for significance. It should be noted that, because the original data were used to select the transformations, this reduces by one the degrees of freedom for significance testing. Twenty-seven of the 49 species gave significant cycles.

RUNNING AVERAGES

Perusal of the original data at all sites showed considerable 'saw tooth' variations between species recordings in consecutive times. To reduce this source of variation, running averages of recordings over two consecutive times were used. These averages were then transformed and annual cyclical regressions were effected.

Results using site 1 data gave 30 of the 49 species with significant cycles. It seems probable that by extending the use of running averages to cover three times, higher average R^2 values could be obtained. This was not effected primarily because of the risk of generating spurious cycles (Cole) 1954. Most future calculations were based on running average data using two consecutive times.

ANNUAL AND NEAR-ANNUAL CYCLES

Originally an interest was declared in annual cycles but after analyses had been completed it was suspected, as in the case of the macrobenthos (Stephenson 1980c) that the near annual periodicity might not be precisely 1 year ($T=13$). A series of cyclical regressions with periodicities of $T=11$ to $T=16$ (with increments of unity) was effected. The numbers of species giving R^2 values which reached levels of significance for each periodicity in each site are given in Table 1.

TABLE 1: NUMBERS OF SPECIES WITH R^2 ABOVE LEVEL FOR SIGNIFICANCE WITH PERIODICITIES OF 11 TO 16 AT EACH OF THE SITES.

Site	Periodicities (13 = 1yr)						Total no. of spp. in sites
	11	12	13	14	15	16	
1	27	31	30	29	27	24	49
2	27	31	30	30	27	26	48
3	36	38	43	45	45	41	53
Sum	90	100	103	104	99	91	150

At sites 1 and 2 the optimal near annual periodicity is 12/13 of a year (48 weeks) but at site 3 it is ca 14·5/13 of a year (1 year and 6 weeks). It is noteworthy that in the present results, as in the macrobenthos from an earlier period, the inshore populations cycle slightly faster than one per year Stephenson 1980c). No satisfactory explanation can be offered.

Overall the results confirmed the selection of one year cycles ($T=13$) for further study.

HALF YEAR CYCLES AND KURTOSIS IN THE DATA

It has been shown earlier (Stephenson 1978) that addition of a half annual cycle to an annual one can mimic a platykurtotic annual cycle and that subtraction can mimic a leptokurtotic cycle.

Cyclical regressions with a half annual cycle ($T=6.5$) were performed on the residuals from annual cycles using site 1 data; these can be assumed to be approximately normally distributed.

The regressions gave an average increment in R^2 values of only 0.197 and overall the effect is negligible. However nine species did give significant increments in R^2, viz. *Leiognathus*, *Charybdis callianassa*, *Thrissocles*, *Johnius*, *Penaeus esculentus*, *Trachypenaeus*, *Saurida undosquamis*, *Platycephalus* and *Portunus sanguinolentus*.

ANNUAL CYCLES ON DATA FROM SINGLE SITES

Results are given in Appendix 2A-C and show that 30 (out of 49) species gave significant cycles at site 1 with the average R^2 0.357, at site 2 the numbers were 30 (out of 48) species with average R^2 0.414, and at site 3 forty-three (out of 53) species with average R^2 0.517.

It is concluded that the preponderant overall trend in the data is conformity with annual cycles, and that the trend becomes more noticeable as one moves from sites 1 and 2 to site 3. This may be partially because of differences in the species which were recorded from the three sites. Average R^2 values were then obtained for those species with significant cycles which occurred at all three sites and these were 0.424, 0.487, and 0.571 for sites 1, 2, and 3 respectively. It is clear that at least part of the difference is due to conditions at the different sites.

Values of the times (0 to 12.9) in which species with significant cycles were estimated to attain their annual maxima are also given in Appendix 2A-C. These times were adjusted to 'real' times, bearing in mind that the running average times were 0.5 units advanced. Plotting frequency distribution diagrams of these times at each site separately showed at most indistinct patterns. Kolmogorov-Smirnov two sample tests failed to show either significant differences or significant similarities between any of the pairs of sites in any of the other regression derivatives.

Twenty-seven species have significant annual cycles at more than one site and these can be grouped as follows with respect to synchrony of cycles:

I. Species at three sites
(a) Nearly synchronised (estimated times of maxima 1 time unit or less apart):
Caranx, *Penaeus esculentus*, *Saurida undosquamis*.
(b) Roughly synchronised (estimated times > 1, < 2.5 apart):
Alpheus stephensoni, *Gerres*, *Oratosquilla anomala*, *Penaeus plebejus*, *Selaroides*, and *Thrissocles*.
(c) Not synchronised (estimated times > 2.5 apart):
Charybdis callianassa, *Leiognathus*, *Loligo*, and *Trachypenaeus*.
II. Species at two sites.
(a) Nearly synchronised (< 1):
Apogonichthys, *Harengula*, *Johnius*, *Metapenaeus bennettae*, *Oratosquilla woodmasoni*, *Paramonacanthus*, *Priopidichthys*, *Sillago ciliata*.
(b) Roughly synchronised (> 1, < 2):
Alima, *Pomatomus*.
(c) Not synchronised (>2.5):
Portunus hastatoides, *Saurida tumbil*, *Scomberomorus*, *Sillago maculata*.

Overall eleven species are nearly synchronised, eight roughly synchronised and eight are not synchronised. No clear patterns emerge within the groups, for example there is no consistent tendency for species which are believed to enter the Bay from the Pacific Ocean to reach their maxima first at site 3 which is in closest contact with the Ocean. There is a hint of a similarity amongst the eight non-synchronised species, five of which are suspected to spend most or all of their life cycles within Moreton Bay, (*Charybdis callianassa*, *Leiognathus*, *Loligo*, *Portunus hastatoides* and *Sillago maculata*). From this is can be argued that in these species within-Bay movements are occurring.

LONGER TERM TIME CHANGES ON SINGLE SITES

The data set showed that a majority of species had lower recordings in the second year of sampling. Paired *t* tests were carried out using transformed data, with pairing of respective times of the two years. Nineteen species had significantly lower catches in the second year at site 1 (site 1 spp. 5, 8, 10, 11, 15, 18, 20, 26, 27, 29, 33, 35, 38, 40, 41, 42, 43, 45, 46). There were 12 equivalent species at site 2 (site 2 spp. 1, 7, 8, 10, 13, 17, 20, 29, 32, 35, 38, 39), and 19 at site 3 (site 3 spp. 4, 6, 7, 10, 11, 15, 20, 23, 25, 27, 30, 33, 34, 36, 38, 39, 43, 49, 50). There was only one example of a significantly increased population in the second year: site 3 sp. 41. It is evident that

there were widespread reductions in populations in the second year of sampling.

It was suspected that cycles were more weakly developed in the data from the second year. At each site annual cyclical regressions were performed separately on each year of data. In these running averages were not used because of the relatively short time periods. The transformations applied to each species were those required to reduce skewness in the two years of data, and not each year separately — this facilitates inter-year comparisons. Results on each of the sites are given in Table 2 and show that fewer species followed cycles in the second year, especially at site 1.

TABLE 2: NUMBER OF SPECIES WITH SIGNIFICANT ANNUAL CYCLES.

Site	Yr. 1	Yr. 2
1	20	6
2	27	13
3	35	19

To evaluate the importance of times changes other than annual cycles in terms of proportions of variance, regressions were performed on the residuals from the cyclical regressions with period 1 year.

Linear regressions of residuals against times showed for site 1, 20 species with significant effects, for site 2 there were 17 and for site 3, 19 species. In each significant case the regression line had a negative slope.

It seems likely that the declines shown in the residuals follow curvilinear rather than linear trends, and while these are likely to follow logistic rather than sinusoidal curves, the latter can be regarded as acceptable mimics of the logistic. Preliminary computations suggested that a cycle of longer than seven years was required and 10 years cycling was arbitrarily chosen. At each of the sites more species showed significant 10 year regressions than linear regressions on the residuals, with numbers at sites 1, 2 and 3 as 29, 24 and 32 respectively (see Appendices 2A–C).

ANALYSES ON DATA SUMMED OVER SITES

Some of the lack of consistency between sites may have been due to random between-site variations. To obtain an overall view, species recordings were summed over sites, and the analyses repeated. Results are given in Appendix 2D.

Of the 70 species all but 18 gave significant annual cycles, and these 18 were concentrated in the lower end of the abundance hierarchy.

Estimated times of attainment of annual maxima in the 52 conforming species are given as a frequency distribution diagram in Fig.1. This shows that 26 of the maxima occur in the 5/13ths of the year between mid October and late February, and that the fewest maxima (1 per four weeks) occur from mid June to mid September. The species with warm weather maxima are: *Charybdis callianassa, Apogon, Loligo, Metapenaeus bennettae, Pomatomus, Caranx, Penaeus*
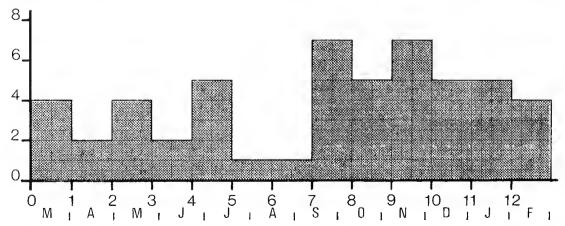

FIG 1: Histogram showing numbers of species (vertically) in pooled catches from sites 1 + 2 + 3 which attained their estimated times of maxima in each 1/13th of the year starting April 1st (horizontally). Times between 0 and 0·99 are given in the interval after zero, and so on until times from 12·0 to 12·99 in the interval after 12. Calendar months also given.

esculentus, Pelates, Gerres, Trachurus, Harengula, Oratosquilla anomala, Saurida tumbil, Selaroides, M. endeavouri, Alpheus stephensoni, Charybdis truncata, Pseudorhombus spp. juv., *Scomberomorus, O. woodmasoni, O. interrupta, Alima, Suggrundus, Odontodactylus, Cepola,* and *Portunus rubromarginatus.*

Ten-year cyclical regressions were carried out on the residuals from annual cycles: 44 species showed significant effects.

CLIMATIC DATA

It seemed possible that the weak annual cycling in the second year was due to climatic irregularities. Climatic data (from Brisbane weather station) for 20 years including the years of sampling, were recompiled so that each year began in March, i.e. the beginning of the month before the first sampling.

Annual rainfall and average temperatures are given in Table 3 together with their conversions to units of standard deviation $+/-$ from the means. In the rainfall data six years gave (absolute) standard deviations of greater than unity (1967, 1968, 1970, 1972, 1977 and 1979); on this basis 1979 (the first year of sampling) had unusually

TABLE 3: ANNUAL RAINFALLS (IN MM) AND ANNUAL AVERAGES OF TEMPERATURES (IN °C) FOR 20 YEARS, EACH BEGINNING MARCH 1ST.

Year	Rainfall		Temperature	
	Yearly total	Units std dev. $+/-$ mean	Average	Units std dev. $+/-$ mean
1961	996	−0·5	20·48	−1·0
62	976	−0·6	20·46	−1·0
63	1338	0·4	20·43	−1·1
64	1115	−0·2	20·65	−0·6
65	1031	−0·4	20·77	−0·4
66	1375	0·5	20·44	−1·1
67	1822	1·8	20·58	−0·8
68	522	−1·8	20·94	0
69	1178	0	21·08	0·3
1970	1970	2·2	20·69	−0·5
71	1144	−0·1	20·61	−0·7
72	1632	1·2	21·01	0·1
73	1056	−0·3	21·77	1·7
74	1492	0·9	20·61	−0·7
75	1148	−0·1	21·02	0·2
76	1076	−0·3	21·28	0·7
77	659	−1·4	21·61	1·4
78	985	−0·5	20·90	−0·1
79	748	−1·2	21·76	1·7
1980	1374	0·5	21·85	1·9
Mean	1181.9		20·95	

low rainfall. In the temperature data 1980 was the warmest year of all, and 1979 was, approximately coequally with 1973, the second warmest year of all. In two years there were both unusual annual rainfalls and unusual temperatures; these were 1977 and 1979.

Data were then considered on a monthly basis and the numbers of months which had weather continuously greater than or less than the monthly averages over the 20 years were noted. The outstanding periods are: for rainfall May 1979 to April 1980, 12 months of low rainfall; and for temperature June 1979 to Nov. 1980, 18 months of high temperatures. In combination there was a continuous period of June 1979 to April 1980 (10 months) in which there were below average rainfalls and above average temperatures. A shorter period of continuously unusual weather with low rainfalls and high temperatures occurred from July to Nov. 1977.

DISCUSSION

The data consisted of recordings of species in three selected sites in Moreton Bay at intervals of four weeks for a two year period. These data were separately analysed on a site by site basis and also using the summed recordings of species in the three sites. Analyses involved determination of running averages of species recordings, transformations to reduce moment coefficients of skewness to as close as possible to 0·5, and annual cyclical regressions.

The main trend in the data was of annual cycling, with this slightly more developed at site 3 than at the other two sites. These differences seem related to abiotic perturbations: deviations from regular seasonal changes in abiotics will almost certainly be greatest at Bramble Bay which is close to the Brisbane River, and least at Middle Banks which is in closest contact with the Pacific Ocean.

Catches of many species were significantly lower and annual cycles were less developed during the second year of sampling. The residuals from annual cycles in many cases showed significant linear declines over time, but a more effective model of the declines was obtained using 10 year cyclical regressions. The declines in population are probably caused by abnormal abiotic conditions. Either the abnormal weather of 1977 is operating after about a 1½ year delay or the abnormal weather of 1979 and 1980 operates with virtually no delay, or there is a combined effect. The present data do not permit choice between these alternatives.

We now view the results from the aspect of assessing changes due to airport construction. It is evident that the present results do not provide an effective baseline. Massive changes have occurred from one year to another without any known or suspected human cause, and comparable if less extreme changes can be expected in the future. One suspects that for an effective baseline study something in excess of 10 years of data would be required. It is unreasonable to expect a lead time of a decade before man-made changes will impinge upon a marine environment.

From the aspect of airport construction it is clearly necessary to consider each site separately. Using data summed over sites led to some clarification, and it was possible to divide the species into two broad groups, those with maximum catches in colder months (18 spp.) and in warmer months (32 spp.) respectively.

In a previous paper (Stephenson, Cook and Newlands, 1978) it was postulated that fish predation had important effects on the macro-benthos. Later work (Stephenson 1980a) showed that the maximum rate of recruitment of the benthos was in August/September and of depletion approximately in December. The latter was attributed to mobile predators or 'disturbers' (fish and prawns), but because only catch data on prawns were available, only relationships between the macrobenthos and prawns could be investigated (Stephenson 1980b). No relevant information on seasonality of fish catches were then available. Seasonal data on the total catches of trawled organisms are now provided, and have been given in Fig. 1 which shows fewest trawled species with a maximum in Aug./Sept. This is the time of maximum benthic recruitment. The present results support the previous work which suggested that benthos is controlled by nekton and nekto-benthic organisms.

Species groupings, based on life styles and/or taxonomic affinities are given in Table 4, and information upon abundances and annual cycles within groups are now considered. (It should be noted that this grouping excludes miscellaneous fish and miscellaneous crustaceans). Significance of annual cycles show some relationships to the taxonomic groups within the catches. Thus all seven stomatopods except the uncommon *Anchisquilla* show highly significant cycles, while three of the six commoner portunids fail to show them. Results on annual cycling of the prawn species can be compared with those obtained by Stephenson and Williams (1981), in analyses of eight years of (weight) catches from Moreton Bay.

There is agreement in the occurrence of significant cycles in the species common to the two lists except for *P. merguiensis* which was sparsely represented in the present catches. However there are noticeable differences between the estimated times of maximum catches by Stephenson and Williams (1981, Table 12) and those obtained in the present work. The latter agree reasonably well with the respective commercial fishing seasons, (see Stephenson and Williams Table 13).

TABLE 4: CONSOLIDATED RESULTS, SPECIES IN ECOLOGICAL OR TAXONOMIC GROUPS. SIGNIFICANCE AT 0·01 LEVEL**, AT 0·05 LEVEL*.

Group	Species	Abundance (2 yr catches)	Annual cycles Signif. Est. time max.
Abundant trash fish	*Leiognathus*	31777	* early Sept.
	Paramonacanthus	20854	** late May
	Apogon	14978	** mid Feb.
	Polynemus	6370	N
Pilchards etc.	*Thrissocles*	1870	** late Oct.
	Hyperlophus	978	N
	Harengula	696	** mid Jan.
Pelagic fish	*Pomatomus*	1381	* mid Feb.
	Caranx	1055	** late Jan.
	Trachurus	720	** mid Nov.
	Selaroides	362	** early Feb.
	Scomberomorus	154	** early March
Bottom dwelling fish	*Callionymus limiceps*	1040	** mid July
	C. belcheri	754	** mid June
	Pseudorhombus sp. juv.	189	** late March
	Platycephalus	114	* early Aug.
	Pseudorhombus arasius	109	* late July
	Suggrundus	98	** late Nov.
	Cynoglossus	25	N
Whiting	*Sillago maculata*	2547	** early Aug.
	S. ciliata	50	** early Nov.
Grinner	*Saurida undosquamis*	2757	** early May
	S. tumbil	471	** mid Jan.
Toad fish	*Spheroides pleurostictus*	252	N
	S. hamiltoni	123	* early June

TABLE 4: (Continued)

Group	Species	Abundance (2 yr catches)	Annual cycles Signif. Est. time max.
Penaeid prawns	*Metapenaeus bennettae*	9449	** early Dec.
	Penaeus plebejus	4415	** mid Oct.
	Trachypenaeus	1074	** mid Feb.
	Metapenaeopsis	1037	** mid Oct.
	P. esculentus	986	** mid Feb.
	Metapenaeus endeavouri	328	** late Dec.
	P. merguiensis	26	N
Portunids	*Charybdis callianassa*	15469	** late Dec.
	Portunus pelagicus	4111	N
	P. hastatoides	1531	N
	P. sanguinolentus	280	N
	C. truncata	222	** mid Dec.
	Thalamita	175	** early Oct.
	P. rubromarginatus	29	** early Dec.
Stomatopods	*Oratosquilla anomala*	588	** mid Dec.
	O. woodmasoni	110	** late Dec.
	O. interrupta	106	** early Jan.
	Alima	104	** late Dec.
	Odontodactylus	69	** mid Jan.
	Anchisquilla	11	N
Alpheids	*Alpheus stephensoni*	296	** mid Nov.
	A. distinguendus	51	N
Scyllarids	*Thenus*	45	N
	Scyllarus	44	N
Cephalopods	*Loligo*	13825	** mid March
	Sepia	135	N
	Octopus	97	* mid July

Within several of the groups in Table 4 there is reasonable consistency in the estimated times within the year of attaining maximum catches. For the pelagic fish with the exception of *Scomberomorus* all maxima occur in summer (mid-November to mid-February), for the bottom fish excepting *Suggrundus* all are in cooler weather (late March to early August), the five penaeids which showed significant cycles gave maxima in late spring to summer (mid-October to mid-February), the four portunids from early October to late December, and the five stomatopods from mid December to mid January.

Finally comments are offered on the relative abundance of the different groups in Table 4 and of the species within them. It is usual in faunistic work for abundances to be given in graded terms

such as 'abundant' and 'very common', but it is unusual for such terms to be derived from data as voluminous as those of the present study. It is easy to arrange all the species in an hierarchical order of abundance and when this has been done (Appendix 2D) the difficulties of separating grades of abundance become evident. Other than dissecting off the first species *(Leiognathus)* and the last *(Anchisquilla)*, there are few obvious break points. Within the groups (see Table 4) discontinuities are more evident, for example *Polynemus* is the lowest numerically abundant trash fish, *Thrissocles* the most abundant pilchard etc., and *Sillago maculata* is the more abundant whiting.

There are constraints on the interpretation of the abundance data in Table 4 for two reasons. The first is that they are likely to be biassed by unusually high recordings during one or another sampling period. This is emphasised by (a) the stringency of transformations required to decrease the skewness of the data, and (b) the knowledge that both absolute and relative abundances change from year to year. This is apparent by comparing Appendix 1 in Stephenson, Chant and Cook (1982) giving first year abundances in heirarchical order with Appendix 2D of the present paper, which gives the abundance heirarchy using two years of data. Any conclusions from the present work need the overall qualification that they apply only to the summated data from the present two years sampling.

Accepting these qualifications and equating values which by subjective judgement appear approximately coequal, abundance hierarchies can be given. Between the thirteen groups of Table 4 the hierarchy with abundances in parenthesis is: abundant trash fish (73979) > portunids (21817) > penaeids (17315) > cephalopods (14057) > pelagic fish (3672) = pilchards (3544) = grinners (3228) > whiting (2597) = bottom fish (2329) > stomatopods (988) > toad fish (375) = alpheids (347) > scyllarids (89). Abundances within the groups of Table 4, provide more precise information than has hitherto been available on a number of taxa. For example the numbers of stomatopods recorded from northern Moreton Bay are greatly in excess of the total numbers of all species recorded from Australian waters by Stephenson and McNeill (1955). We can now arrange species in the following hierarchy: *Oratosquilla anomala* (588) > *O. woodmasoni* (110) = *O. interrupta* (106) = *Alima* (104) > *Odontodactylus* (69) > *Anchisquilla* (11). A similar lack of precision applied to data on

portunids (see Stephenson 1972 for literature). The species in the present collection can be arranged as follows: *Charybdis callianassa* (15469) > *Portunus pelagicus* (4111) > *P. hastatoides* (1531) > *P. sanguinolentus* (280) > *C. truncata* (222) > *Thalamita* (175) > *P. rubromarginatus* (29).

A grouping alternative to that of Table 4 would be into species caught for the market (prawns, *Portunus pelagicus*, alpheids, *Thenus, Loligo* and say half of *Sillago* spp.), those of no commercial value (e.g. trash fish), and those of 'negative value' in the sense of removal and non-sale of fish caught by other techniques (e.g. angling). The approximate respective numbers in these groups taken from Table 4 (i.e. excluding miscellaneous fish and crustaceans) are: 36923, 102313, 5085. The direct damage to angling fish comprises only 3·5% of the total catch, and a relatively large proportion of trawled individuals is wasted from an economic viewpoint (74%).

ACKNOWLEDGEMENTS

APPENDIX 1

SPECIES LIST
The 70 species considered, in alphabetical order. Authors and systematic positions given only for species not listed in Stephenson, Chant & Cook (1982).

Adenopogon rosiegaster (Ramsay & Ogilby), Apogonidae, Pisces; *Alima laevis; Alpheus distinguendus; A. stephensoni; Anchisquilla fasciata* (de Haan), Stomatopoda, Crustacea; *Apogon quadrifasciatus; Apogonichthys ellioti; Callionymus belcheri; C. limiceps; Caranx malam; Centropogon marmoratus; Cepola australis* Ogilby, Cepolidae, Pisces; *Charybdis callianassa; C. truncata; Cynoglossus bilineatus* (Lacépède), Cynoglossidae, Pisces; *Dorippe australiensis; Euristhmus lepturus; Gerres ovatus; Harengula castelnaui; Hyperlophus translucidus; Johnius australis; Leiognathus moretonensis; Loligo formosana; Metapenaeopsis novae-guinae; Metapenaeus bennettae; M. endeavouri; Minous versicolor; Neoarius australis* (Günther), Trachysuridae, Pisces; *Octopus membranaceus; Odontodactylus cultrifer; Oratosquilla anomala; O. interrupta; O. woodmasoni; Paramonacanthus oblongus; Parapercis nebulosus* (Quoy & Gaimard), Parapercidae, Pisces; *Pelates quadrilineatus; Penaeus esculentus; P. merguiensis* de Man, Penaeidea, Crustacea; *P. plebejus; Phalangipus australiensis; Platycephalus indicus; Polynemus multiradiatus; Pomatomus saltatrix; Portunus hastatoides; P. pelagicus; P. rubromarginatus* (Lanchester), Portunidae, Crustacea; *P. sanguinolentus; Priacanthus macracanthus; Priopidichythys marianus; Pseudorhombus arsius; Pseudorhombus* spp. (juvs); *Saurida tumbil; S. undosquamis; Scomberomorus queenslandicus; Scyllarus tuberculatus* (Bate), Scyllaridae, Crustacea; *Selaroides leptolepis; Sepia aculeata; Siganus spinus; Sillago ciliata* Cuvier, Sillaginidae, Pisces; *S. maculata; Spheroides hamiltoni; S. pleurostictus; Sphyraena obtusata; Suggrundus harrisii; Thalamita sima; Thenus orientalis; Thrissocles hamiltoni; Trachurus mccullochi; Trachypenaeus fulvus; Upeneus tragula.*

APPENDIX 2
Results of regressions: A site 1, B site 2, C site 3, and D sites 1 + 2 + 3. Significance at 0·05 level *, at 0·01 level **.

APPENDIX 2A: SITE 1

Code No.	Species	Abundance (sum over 26 times)	1 yr Cyclical regressions			10 yr Cyc. regr. on resids from 1 yr R^2
			Root transf	R^2	Adjusted est time max	
1	*Leiognathus*	4593	8	0·450**	12·7	0·299*
2	*Metapenaeus bennettae*	3844	2	0·181		0·364*
3	*Charybdis callianassa*	3786	1	0·467**	10·0	0·243
4	*Penaeus plebejus*	3404	2	0·775**	6·9	0·004
5	*Apogon*	3071	1	0·002		0·531**
6	*Polynemus*	2463	1	0·178		0·257
7	*Loligo*	2311	1	0·653**	11·9	0·028
8	*Portunus pelagicus*	1512	3	0·378**	8·4	0·659**

9	*Thrissocles*	1051	3	0·345*	7·2	0·134
10	*Pelates*	921	2	0·289*	11·0	0·530**
11	*Sillago maculata*	691	1	0·312*	2·8	0·435**
12	*Johnius*	633	2	0·424**	7·4	0·136
13	*Harengula*	550	1	0·377**	10·2	0·570**
14	*Gerres*	525	3	0·709**	10·6	0·321*
15	*Hyperlophus*	486	2	0·104		0·514**
16	*Sphyraena*	462	1	0·377**	1·7	0·158
17	*Penaeus esculentus*	299	1	0·526**	12·2	0·075
18	*Pomatomus*	296	1	0·756**	10·5	0·537**
19	*Trachypenaeus*	279	3	0·334*	6·5	0·030
20	*Paramonacanthus*	211	3	0·237		0·271
21	*Spheroides pleurostictus*	179	3	0·052		0·354*
22	*Adenopogon*	166	4	0·332*	2·8	0·434**
23	*Caranx*	158	3	0·825**	11·3	0·323*
24	*Oratosquilla anomala*	133	1	0·465**	7·4	0·033
25	*Centropogon*	131	1	0·254		0·172
26	*Thalamita*	98	2	0·405**	5·8	0·675**
27	*Euristhmus*	84	2	0·130		0·418**
28	*Priopidichthys*	83	3	0·735**	7·7	0·097
29	*Selaroides*	73	8	0·359*	12·5	0·345*
30	*Alima*	64	2	0·368*	9·2	0·292*
31	*Alpheus stephensoni*	61	3	0·749**	7·2	0·027
32	*Apogonichthys*	53	2	0·032		0·424**
33	*Dorippe*	52	3	0·177		0·639**
34	*Spheroides hamiltoni*	50	1	0·435**	1·9	0·631**
35	*Scyllarus*	44	3	0·003		0·298*
36	*Scomberomous*	43	3	0·130		0·608**
37	*Saurida undosquamis*	41	8	0·717**	2·0	0.278
38	*Phalangipus*	38	1	0·064		0·571**
39	*Sillago ciliata*	38	2	0·356*	7·7	0·483**
40	*Siganus*	37	4	0·429**	0·7	0·514**
41	*Sepia*	34	2	0·073		0·661**
42	*Upeneus*	32	2	0·511**	1·5	0·433**
43	*Thenus*	27	4	0·215		0·607**
44	*Penaeus merguiensis*	26	2	0·186		0·049
45	*Platycephalus*	24	2	0·589**	4·9	0·245
46	*Pseudorhombus arsius*	23	8	0·204		0·801**
47	*Portunus sanguinolentus*	14	8	0·597**	0·6	0·162
48	*Neoarius*	12	1	0·083		0·017
49	*P. hastatoides*	12	2	0·162		0·216

APPENDIX 2B: SITE 2

1	*Paramonacanthus*	14793	8	0·370**	1·8	0·569**
2	*Leiognathus*	14515	2	0·540**	3·4	0·411**
3	*Charybdis callianassa*	10566	3	0·741**	8·9	0·618**
4	*Metapenaeus bennettae*	5283	6	0·669**	9·4	0·017
5	*Loligo*	4508	3	0·791**	0·9	0·166
6	*Apogon*	3711	5	0·290*	10·7	0·301*
7	*Polynemus*	3216	3	0·281*	11·4	0·296*
8	*Portunus pelagicus*	1458	8	0·030		0·806**
9	*Pomatomus*	859	2	0·145		0·356*
10	*Portunus hastatoides*	609	5	0·327*	2·7	0·753**
11	*Penaeus plebejus*	588	2	0·837**	8·6	0·191

12	*Thrissocles*	511	1	0·613**	9·5	0·034
13	*Hyperlophus*	492	4	0·103		0·350*
14	*Trachurus*	425	5	0·643**	8·6	0·156
15	*Trachypenaeus*	406	2	0·391**	10·3	0·519**
16	*P. esculentus*	324	2	0·886**	11·3	0·236
17	*Saurida undosquamis*	291	2	0·707**	1·2	0·484**
18	*Portunus sanguinolentus*	266	5	0·203		0·758**
19	*Johnius*	246	1	0·189		0·055
20	*Sillago maculata*	206	2	0·105		0·426**
21	*Caranx*	204	4	0·752**	10·5	0·236
22	*Alpheus stephensoni*	201	7	0·792**	9·4	0·165
23	*Harengula*	146	8	0·476**	10·0	0·181
24	*Apogonichthys*	139	5	0·386**	0·9	0·282
25	*Oratosquilla anomala*	106	2	0·732**	9·3	0·433**
26	*Spheroides pleurostictus*	72	4	0·346*	7·5	0·057
27	*Gerres*	71	2	0·611**	9·2	0·165
28	*Scomberomorus*	59	1	0·617**	12·1	0·680**
29	*Sepia*	50	3	0·093		0·714**
30	*Callionymus limiceps*	48	2	0·218		0·121
31	*Selaroides*	46	5	0·464**	11·7	0·190
32	*Saurida tumbil*	42	4	0·428**	3·8	0·707**
33	*Spheroides hamiltoni*	41	1	0·047		0·307*
34	*Alima*	40	2	0·668**	10·4	0·268
35	*Priacanthus*	37	3	0·013		0·522**
36	*Sphyraena*	37	4	0·061		0·571**
37	*Thalamita*	34	2	0·792**	8·9	0·169
38	*Alpheus distinguendus*	31	4	0·078		0·727**
39	*Euristhmus*	26	8	0·225		0·494**
40	*Neoarius*	26	8	0·697**	1·1	0·234
41	*Priopidichthys*	23	5	0·708**	8·4	0·199
42	*Oratosquilla woodmasoni*	20	4	0·529**	9·1	0·169
43	*C. belcheri*	19	2	0·027		0·129
44	*Siganus*	18	8	0·241		0·580**
45	*Pseudorhombus* spp. juvs	15	8	0·122		0·090
46	*O. interrupta*	14	5	0·210		0·275
47	*Pelates*	12	1	0·204		0·324*
48	*Sillago ciliata*	12	2	0·451**	8·4	0·263

APPENDIX 2C: SITE 3

1	*Leiognathus*	12589	1	0·748**	7·1	0·145
2	*Apogon*	8196	1	0·322*	11·6	0·239
3	*Loligo*	7481	8	0·590**	11·8	0·825**
4	*Paramonacanthus*	5850	2	0·706**	1·9	0·571**
5	*Saurida undosquamis*	2460	2	0·760**	1·0	0·077
6	*Sillago maculata*	1650	6	0·590**	5·2	0·532**
7	*Portunus pelagicus*	1124	8	0·037		0·714**
8	*Charybdis callianassa*	1071	3	0·499**	11·7	0·549**
9	*Metapenaeopsis*	1035	3	0·830**	7·0	0·258
10	*Callionymus limiceps*	992	1	0·444**	3·5	0·534**
11	*P. hastatoides*	910	7	0·447**	7·3	0·511**
12	*C. belcheri*	735	2	0·634**	2·6	0·410**
13	*Caranx*	694	1	0·832**	10·8	0·187
14	*Polynemus*	629	2	0·510**	8·2	0·575**
15	*Apogonichthys*	601	2	0·467**	0·8	0·393**

16	*Saurida tumbil*	429	3	0·642**	10·5	0·345*
17	*Penaeus plebejus*	423	1	0·816**	7·4	0·268
18	*Trachypenaeus*	389	2	0·694**	7·2	0·265
19	*P. esculentis*	363	2	0·771**	11·4	0·532**
20	*Oratosquilla anomala*	350	2	0·917**	9·6	0·212
21	*Priacanthus*	339	3	0·606**	1·0	0·579**
22	*Metapenaeus endeavouri*	328	2	0·714**	9·8	0·226
23	*M. bennettae*	322	4	0·786**	8·6	0·499**
24	*Thrissoccles*	308	4	0·769**	7·5	0·107
25	*Trachurus*	295	2	0·174		0·353*
26	*Gerres*	265	2	0·909**	8·5	0·255
27	*Centropogon*	247	2	0·558**	3·9	0·396**
28	*Selaroides*	243	2	0·694**	10·8	0·642**
29	*Charybdis truncata*	222	3	0·518**	9·3	0·521**
30	*Pomatomus*	212	3	0·620**	9·1	0·645**
31	*Pseudorhombus* spp. juvs	175	2	0·625**	0·2	0·016
32	*Suggrundu*	98	1	0·538**	8·7	0·048
33	*Octopus*	97	2	0·285*	3·5	0·455**
34	*Oratosquilla interrupta*	92	2	0·643**	10·1	0·547**
35	*O. woodmasoni*	90	1	0·584**	9·1	0·053
36	*P. arsius*	86	2	0·317*	4·5	0·634**
37	*Platycephalus*	80	1	0·060		0·304*
38	*Minous*	74	1	0·061		0·235
39	*Upeneus*	73	2	0·047		0·652**
40	*Odontodactylus*	69	1	0·740**	10·4	0·002
41	*Johnius*	53	2	0·647**	8·1	0·111
42	*Scomberomorus*	52	8	0·325*	10·6	0·593**
43	*Sepia*	51	3	0·323*	0·9	0·657**
44	*Thalamita*	43	2	0·085		0·025
45	*Alpheus stephensoni*	34	8	0·571**	7·9	0·331*
46	*Cepola*	33	3	0·754**	12·2	0·314*
47	*Spheroides hamiltoni*	32	1	0·173		0·141
48	*Portunus rubromarginatus*	29	2	0·839**	8·9	0·332*
49	*Parapercis*	27	1	0·337*	4·0	0·363*
50	*Cynoglossus*	25	2	0·213		0·617**
51	*A. distinguendus*	20	5	0·213		0·546**
52	*Thenus*	18	5	0·312*	3·4	0·226
53	*Anchisquilla*	11	1	0·088		0·170

APPENDIX 2D: ALL SITES

All sites code no.	Species	No.	Sites of occurrence	Annual cycles		
				Root transf	R^2	T max (adjusted)
1	*Leiognathus*	31777	1,2,3	1	0·292*	5·5
2	*Paramonacanthus*	20854	1,2,3	8	0·591**	2·1
3	*Charybdis callianassa*	15469	1,2,3	2	0·828**	9·8
4	*Apogon*	14978	1,2,3	8	0·341*	11·3
5	*Loligo*	13825	1,2,3	8	0·717**	12·5
6	*Metapenaeus bennettae*	9449	1,2,3	1	0·512**	8·8
7	*Polynemus*	6370	1,2,3	2	0·154	
8	*Penaeus plebejus*	4415	1,2,3	1	0·746**	7·0
9	*Portunus pelagicus*	4111	1,2,3	3	0·029	
10	*Saurida undosquamis*	2757	1,2,3	2	0·789**	1·1
11	*Sillago maculata*	2547	1,2,3	4	0·412**	4·4

12	*Thrissocles*	1870	1,2,3	2	0·503**	7·6
13	*Portunus hastatoides*	1531	1,2,3	8	0·103	
14	*Pomatomus*	1381	1,2,3	1	0·281*	11·5
15	*Trachypenaeus*	1074	1,2,3	2	0·461**	7·9
16	*Caranx*	1055	1,2,3	2	0·878**	10·8
17	*Callionymus limiceps*	1040	2,3	1	0·439**	3·6
18	*Metapenaeopsis*	1037	3	3	0·831**	7·0
19	*Penaeus esculentus*	986	1,2,3	1	0·837**	11·5
20	*Hyperlophus*	978	1,2	3	0·116	
21	*Pelates*	933	1,2	2	0·289*	11·1
22	*Johnius*	932	1,2,3	2	0·349*	7·8
23	*Gerres*	861	1,2,3	2	0·790**	9·8
24	*Apogonichthys*	793	1,2,3	3	0·433**	0·8
25	*Callionymus belcheri*	754	2,3	3	0·665**	2·7
26	*Trachurus*	720	2,3	2	0·580**	8·2
27	*Harengula*	696	1,2	2	0·548**	10·2
28	*Oratosquilla anomala*	588	1,2,3	1	0·844**	9·3
29	*Sphyraena*	499	1,2	1	0·265*	1·9
30	*Saurida tumbil*	471	2,3	3	0·432**	10·4
31	*Centropogon*	378	1, 3	1	0·432**	4·2
32	*Priacanthus*	376	2,3	3	0·502**	0·8
33	*Selaroides*	362	1,2,3	3	0·719**	11·1
34	*Metapenaeus endeavouri*	328	3	2	0·714**	9·8
35	*Alpheus stephensoni*	296	1,2,3	3	0·728**	8·4
36	*Portunus sanguinolentus*	280	1,2	5	0·217	
37	*Spheroides pleurostictus*	252	1,2,	1	0·018	
38	*Charybdis truncata*	222	3	3	0·518**	9·3
39	*Neoarius*	198	1,2	5	0·411**	0·2
40	*Pseudorhombus* spp. juvs	189	2,3	1	0·613**	12·9
41	*Thalamita*	175	1,2,3	1	0·347*	6·8
42	*Adenopogon*	166	1	4	0·341*	2·8
43	*Scomberomorus*	154	1,2,3	3	0·484**	12·0
44	*Sepia*	135	1,2,3	2	0·085	
45	*Spheroides hamiltoni*	123	1,2,3	1	0·267*	2·4
46	*Euristhmus*	120	1,2,3	2	0·054	
47	*Platycephalus*	114	1, 3	1	0·313*	4·6
48	*O. woodmasoni*	110	2,3	1	0·573**	9·5
49	*Pseudorhombus arsius*	109	1, 3	2	0·287*	4·1
50	*Priopidichthys*	106	1,2	3	0·813**	7·8
51	*O. interrupta*	106	2,3	2	0·619**	10·1
52	*Upeneus*	105	1, 3	2	0·179	
53	*Alima*	104	1,2	2	0·645**	9·8
54	*Suggrundus*	98	3	1	0·538**	8·7
55	*Octopus*	97	3	2	0·285*	3·5
56	*Minous*	74	3	1	0·061	
57	*Odontodactylus*	69	3	1	0·740**	10·4
58	*Siganus*	55	1,2	6	0·423**	0·7
59	*Dorippe*	52	1	3	0·178	
60	*Alpheus distinguendus*	51	2,3	2	0·152	
61	*Sillago ciliata*	50	1,2	2	0·480**	7·7
62	*Thenus*	45	1, 3	3	0·256	
63	*Scyllarus*	44	1	3	0·009	
64	*Phalangipus*	38	1	1	0·070	
65	*Cepola*	33	3	3	0·754**	12·2
66	*Portunus rubromarginatus*	29	3	2	0·839**	8·9

67	*Parapercis*	27		3		1	0·337*	4·0
68	*Penaeus merguiensis*	26	1			2	0·175	
69	*Cynoglossus*	25		3		2	0·213	
70	*Anchisquilla*	11		3		1	0·088	

LITERATURE CITED

BURGESS, D.A., 1980. 'Numerical Analyses of Demersal Fish Assemblages in Northern Moreton Bay, Queensland.' Unpublished M.Sc. thesis. Zoology Department, University of Queensland.

COLE, L.C., 1954. Some features of random population cycles. *J. Wildl.Mgmt.* **18**: 2–24.

PEARSON, E.S. and H.O. HARTLEY, 1966. 'Biometrika Tables for Statisticians'. 3rd edn. Vol.1. Cambridge: Cambridge University Press, p.67-9.

STEPHENSON, W., 1972. An annotated check list and key to the Indo-West-Pacific Swimming Crabs (Crustacea: Decapoda: Portunidae). *Bull. Roy. Soc. N.Z.* **10**: 1–64.

1978. Analyses of periodicity in macrobenthos using constructed and real data. *Aust. J. Ecol.* **3**: 321–36.

1980a. Flux in the sublittoral macrobenthos of Moreton Bay. *Aust. J. Ecol.* **5**: 95–116.

1980b. Relationships of the macrobenthos of Moreton Bay to prawns and to abiotic factors. *Aust. J. Ecol.* **5**: 143–9.

1980c. Time patterns of macrobenthic species in Moreton Bay. *Aust. J. Ecol.* **5**: 245–62.

and BURGESS., 1980. Skewness of data in the analyses of species in sites in times. *Proc. Roy. Soc. Qd* **91**: 37–52.

CHANT, D.C. and S.D. COOK, 1982. Trawled catches in Northern Moreton Bay, 1. Effects of sampling variables. *Mem. Qd. Mus.* **20**: 375–86.

COOK, S.D. and S.J. NEWLANDS, 1978. The macrobenthos of the Middle Banks area of Moreton Bay. *Mem. Qd. Mus.* **18**: 185–212.

and F. MCNEILL, 1955. The Australian Stomatopoda (Crustacea) in the collections of the Australian Museum, with a check list and key to the known Australian species. *Rec. Aust. Mus.* **25**: 239–65.

and M.J. WILLIAMS, 1981. Analyses of South Queensland prawn catches landed at Queensland Fish Board depots. *Proc. Roy. Soc. Qd* **92**: 57–74.

HYMENOSOMATID CRABS OF QUEENSLAND ESTUARIES AND TIDAL MUD FLATS, INCLUDING DESCRIPTIONS OF FOUR NEW SPECIES OF *ELAMENOPSIS* A. MILNE-EDWARDS AND A NEW SPECIES OF *AMARINUS* LUCAS.

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ABSTRACT

Five new hymenosomatid species, *Elamenopsis thorsbornei* n.sp., *E. hirtirostris* n.sp., *E. minima* n.sp., *E. frontalis* n.sp. and *Amarinus lutarius* n.sp. are described. An ovigerous female of *E. minima* n.sp. is 1·7mm carapace width, probably the smallest mature female brachyuran ever reported. Fourteen hymenosomatid species are now known from Queensland estuaries and tidal mud flats. Of these, four are temperate – subtropical Australian species extending into southern or central Queensland, eight are essentially tropical species, and two species occur all along the Queensland coast and beyond. Five species are known only from single or adjacent localities, and the maximum number of species known from any one estuary is five. A key to the Australian species of *Amarinus* is given.

INTRODUCTION

Queensland has a large number of estuaries, allied with extensive areas of mangroves and mud flats. In common with other such areas in the Indo-west Pacific, the macroscopic crab fauna of these habitats is dominated by species of the families Ocypodidae and Grapsidae. There are however, also a number of much smaller species belonging to the family *Hymenosomatidae* Macleay. The hymenosomatids are small to very small, cryptic due to generally dull colouration and accumulation of silt on their bodies, and inactive and often buried during low tides. For these reasons they are often overlooked even though they may be very abundant. Plankton studies of one Queensland river showed the larvae of *Elamenopsis lineata* A. Milne-Edwards 1873 to be the most numerically abundant of all meroplanktonic decapod larvae over an eight month study period (Chaloupka 1978).

Lucas (1980) recorded nine species of Hymenosomatidae from Queensland. He acknowledged that the northern Australian coastal region was poorly collected and expected that more new species would be found. This expectation has already been fulfilled by collections from recent biological surveys of several Queensland estuaries and the new records and new species are presented here.

The material examined is held at the Queensland Museum (QM), the museum of the School of Biological Sciences, James Cook University (JCU) and Allan Hancock Foundation, California, U.S.A. (AHF). Terminology follows the convention of Melrose (1975, fig. 1) (repeated by Lucas, 1980, fig. 1). The general measure of size is maximum carapace width (CW) in millimetres (mm) (including lateral walls), which is usually about the level of the posterior lateral angles of the carapace. Descriptions are based on mature females and large males (see Lucas 1980, p .150) unless otherwise stated. (See Melrose (1975, p. 11) and Lucas (1980, p. 150) for comments on allometric growth in hymenosomatids.)

Family HYMENOSOMATIDAE MacLeay 1838

HYMENOSOMA Desmarest 1825

Hymenosoma hodgkini Lucas 1980

Hymenosoma hodgkini Lucas, 1980, p.169–70, figs. 2E, 6H, 7I, 10B, C.

MATERIAL EXAMINED

Burnett River, 20.x.1980, R.G. Pearson and L.K. Penridge, 2 ovigerous ♀ ♀ (4·3, 5·4 mm), dredge sample, (sample included *Halicarcinus bedfordi),* barrage sample (JCU); Kolan River, 21.x.1980, 6 ♂ ♂ (4·1 – 5·6 mm), ovigerous ♀ (4·7 mm), 4 immature ♀ ♀ (3·5 – 4·2 mm), dredge samples (JCU); Calliope River, Feb. 1976, P. Saenger, 2 ovigerous ♀ ♀ (4·3, 4·4 mm), 14 km from mouth, channel (QM W6908); Calliope River, Aug. 1976, P. Saenger, 2 ♂ ♂ (4·5, 5·2 mm), ovigerous ♀ (4·0 mm), immature ♀ (3·9 mm), 14 km from mouth, edge of channel (QM W6815).

DIAGNOSIS

Dorsal carapace surface with well defined grooves; rostrum much shorter than eye, not reaching cornea; without an epistome; dactyli of walking legs with a row of fine teeth; mature female abdomen projecting posteriorly in two large bulges at segment 3.

DISTRIBUTION

Coastal marine lakes, inlets and estuaries from Western Port, Victoria, to Calliope River, central Queensland.

REMARKS

The known distribution of this species is considerably extended here to include all of the temperate eastern coast of Australia. In addition to the material above, specimens have been examined from Bancroft Bay, Gippsland Lakes, and Waratah Bay, Victoria. G.C. Poore (pers. comm.) reports the species as common in Mallacoota Inlet, Lake Victoria and Lake King (Gippsland Lakes), but uncommon in Western Port and not known from Port Phillip Bay.

HALICARCINUS White 1846

Halicarcinus bedfordi Montgomery 1931

Hymenosoma sp: Montgomery, 1921, p.94–5.
Halicarcinus bedfordi Montgomery, 1931, p.425–6, pl. 27, figs. 3, 3a,b. Melrose, 1975, p.82. Lucas, 1980, p.181–2, figs. 3A, 5E, 6N, 7G, 9E, F.

MATERIAL EXAMINED

Susan River, 26.xii.1970, Australian Littoral Soc., ovigerous ♀ (2·8 mm), (QM W8949); Bogimbah Ck., Fraser Island, 22.vii.1975, R. Timmins and P. Davie, immature ♀ (2·2 mm), sieved from mud flat (QM W6424); Burnett River, 20.x.1980, R.G. Pearson and L.K. Penridge, 2 ♂ ♂ (4·0, 4·7 mm), ovigerous ♀ (4·2 mm), dredge sample, (sample included *Hymenosoma hodgkini)* (JCU); Calliope River, 7–9.x.1975, P. Saenger, 2 ovigerous ♀ ♀ (4·1, 4·8 mm), 10·5 km from mouth, edge of channel (QM W6902); Trinity Inlet, Cairns, Dec. 1974, R. Timmins, 5 ♂ ♂ (4·0 – 5·2 mm), ovigerous ♀ (4·0 mm) (QM W4581); Trinity Inlet, Cairns, 14.xii.1975, Aust. Litt. Soc., ♂ (2·7 mm) (QM W7430).

DIAGNOSIS

Rostrum approximately triangular, narrowing abruptly half-way or further along its length, terminating in a rounded point; eyes reaching to at least 0·4 length of rostrum; without a spine at posterior lateral angle; chelipeds massive and elongate in large males, 3 X or more carapace width; male abdomen almost equilateral triangular; male first pleopods with broad base and stout straight distal portion, terminating in a broad rounded point with tufts of long setae arising subterminally.

DISTRIBUTION

Queensland and Western Australia; specimens reported from Shark Bay and the Swan River in Western Australia, and in Queensland from Weipa, and from Cairns south to Moreton Bay. It presumably has a circum-northern distribution.

ELAMENOPSIS A. Milne-Edwards 1873

Elamenopsis lineata A. Milne-Edwards 1873

Elamenopsis lineatus A. Milne-Edwards, 1873, p. 324–5, pl. 18, fig. 4. Kemp, 1917, p. 250. Tesch, 1918, p. 26–8, pl. l, figs. 5, 5a–c. Serene and Umali, 1970, p. 58, pl. 5, fig. 11.
Elamenopsis lineata: Lucas, 1980, p. 192–3, figs. 3J, 5J, 8E, 10J.

MATERIAL EXAMINED

Calliope River, Dec. 1975, P. Saenger, juvenile ♂(1·8 mm), cooling water outlet at Power Station, edge of channel (QM W6909); Ross River, north Queensland, 4.x.1980, M. Kenway, ovigerous ♀ (7·2 mm), between Bundy Creek and National

Park boat ramp, in entrance of *Callianassa australiensis* burrow, approx. 80 m out from *Rhizophora* edge, sandy mud substrate (JCU); Murray River, north of Cardwell, NE Queensland, 24.v.1978, P. Davie, juvenile, ♂ (3·2 mm), immature ♀ (3·0 mm), benthic grab samples, muddy-sand and mud substrates (QM W7805, W7806); Trinity Inlet, Cairns, Dec. 1974, R. Timmins, ♂ (3·5 mm), (QM W4582).

DIAGNOSIS

Carapace wider than long, approximately hexagonal; rostrum triangular with rounded apex, strongly deflexed and nearly perpendicular; walking legs broad and laterally compressed, dactyli without teeth; fused section of male abdomen tapering, not constricted abruptly.

DISTRIBUTION

New Caledonia; eastern Australia south to Lake Macquarie; Philippines.

REMARKS

The female specimen from Ross River is unusual for its large size (about twice the carapace width of previously reported mature females) and for occupying the burrow of another decapod crustacean, the 'yabby' *Callianassa australiensis*.

Chaloupka (1978) found that the distinctive larvae of *E. lineata* were the most numerically abundant of all meroplanktonic decapod larvae in Ross River estuary over the period February to October, 1978. This abundance of larvae, despite the low fecundity of this small species, suggests that the crabs are very abundant in Ross River while remaining very inconspicuous. It is notable that the next most abundant decapod larvae in Chaloupka's samples were those of the yabby, *C. australiensis*, which reaches densities greater than 100/m² in regions of Ross River (Kenway, 1980) and has egg masses at least a magnitude larger than those of *E. lineata*.

In addition to the material above, specimens of *E. lineata* from Lake Macquarie, N.S.W., have been examined. This record extends the known distribution considerably down the eastern Australian coast.

Elamenopsis octagonalis (Kemp 1917)
(Fig. 4)
Rhynchoplax octagonalis Kemp, 1917, p. 256–8, fig. 5.
Neorhynchoplax octagonalis: Sakai, 1938, p. 2.
Elamenopsis octagonalis: Lucas, 1980, p. 193–4, figs. 4A, 6P.

MATERIAL EXAMINED

Dunwich, Stradbroke Island, Moreton Bay, 17.iv.1973 and 4.v.1973, J.S. Garth, 4 ♂♂ (2·3–3·7 mm, right 1st pleopod of largest male detached and mounted on slide), 3 ♀♀ (3·1–3·4 mm), immature ♀ (2·4 mm), (AHF 1530–04, 1534–04); Moreton Bay, Goat and Bird Islands, 1.v.1973, J.G. Garth, immature ♀ (2·9 mm), (AHF 1531–03); Jacksons Ck., Cribb Is., Moreton Bay, 19.vii.1973, B. Campbell, ♂ (2·6 mm), mouth, north bank (QM W4519).

DIAGNOSIS

Carapace approximately octagonal; lateral carapace walls with a forward directed spine above base of 1st walking leg; rostrum consisting of three separate spine-like lobes, fringed with short setae, lateral lobes well spaced from medial lobe, pointing slightly upward and outward, medial lobe longest, pointing forward; walking legs not laterally compressed, dactyli with one subterminal tooth; distal portion of male 1st pleopod tapering to point, with row of setae on sternal side.

DISTRIBUTION

Goa, India; Moreton Bay, Queensland.

Elamenopsis aspinifera Lucas 1980
Elamenopsis aspinifera Lucas, 1980, p. 195–6, figs. 3I, 5G, 6R, 8D, 10G.

MATERIAL EXAMINED
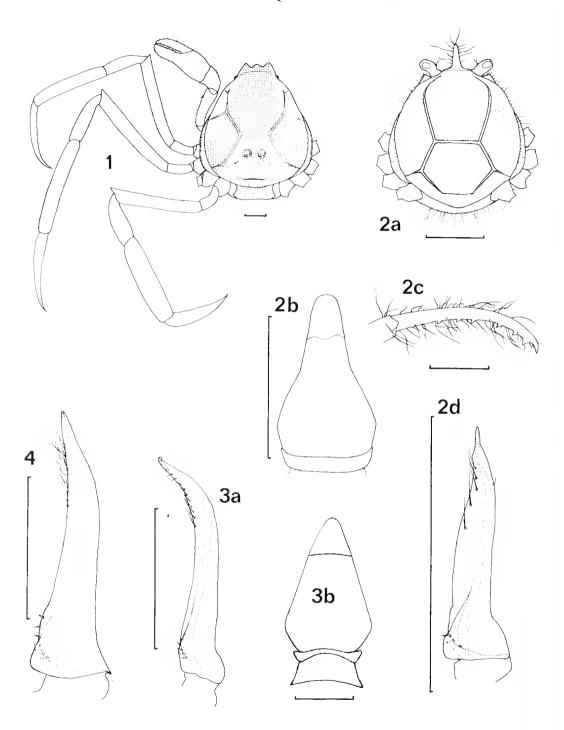
Murray River, north of Cardwell, NE Queensland, 17.v.1978, P. Davie, 2 immature ♀♀ (2·3, 2·5 mm), south bank, downstream from Tomahawk Bend, thick mud (QM W7803).

DIAGNOSIS

Carapace subcircular, lateral carapace walls without spines; rostrum consisting of three separate spinelike lobes, fringed with short setae, lateral lobes well spaced from medial lobe, pointing slightly upward, medial lobe longest, pointing forward; walking legs not laterally compressed, dactyli without subterminal teeth; male 1st pleopod with thin terminal portion short and terminating bluntly.

DISTRIBUTION

Northern Queensland, from Ross River to Weipa.

FIGS. 1–4: 1. *Elamenopsis thorsbornei* n. sp., dorsal view, Holotype; 2. *E. minima* n. sp., (a) dorsal view, Holotype (b) male abdomen (not including first segment), Paratype (c) dactyl of third walking leg, Paratype (d) first male pleopod (lateral view of right side of right pleopod), Paratype; 3. *E. torrensica,* (a) first male pleopod (b) male abdomen; 4. *E. octagonalis,* first male pleopod. Scales: 1, 2a, 3b = 1 mm; 2b, c, d, 3a, 4 = 0·5 mm.

Elamenopsis torrensica Lucas 1980
(Fig. 3a, b)
Elamenopsis torrensica Lucas, 1980, p. 194–5,
figs. 4B, 6Q.

MATERIAL EXAMINED
Field Island, mouth of South Alligator River,
Northern Territory, 3.iii.1979, P. Davie, ♂ (c. 2·2
mm), ♀♀ (2·8, 2·8 mm), in coral rubble on
sandy mud flat in front of mangroves (QM
W8965).

DIAGNOSIS
Carapace approximately octagonal; lateral
carapace walls without spines or crests; rostrum
consisting of three rounded lobes which are
narrow and separate, without fringing setae,
lateral lobes well spaced from medial lobe,
pointing slightly upward, curving slightly inward,
medial lobe longest, pointing forward; walking
legs not laterally compressed, dactyli with one
subterminal tooth.

DISTRIBUTION
Northern Australia (known only from Torres
Strait, and Field Is., N.T.).

REMARKS
This species was previously known only from
the female type specimen. Thus these specimens
provide details of male morphology and further
details of female morphology for specimens which
are somewhat smaller than the holotype, although
they are also apparently mature individuals.
Male chelipeds c. 1·25 X carapace width,
slightly longer and slightly more inflated than
chelipeds of ♀♀ in this sample, fingers with three
low teeth on each cutting edge; walking legs
slender and elongate, length of walking leg 2 c. 3
X carapace width in ♂ and c. 2·5 X carapace
width in ♀♀; ♀ abdomen with tuft of long setae at
abdominosternal junction, suture between seg-
ments 4 and 5 visible; ♂ abdomen typical of genus,
segment 2 short, fused article of segments 3–5
expanding proximally to widest point of abdomen
and then tapering to telson, telson approximately
equilateral triangular with rounded apex and tuft
of setae (abdomen somewhat distorted in this
specimen); ♂ 1st pleopod moderately slender,
distally curved towards sternum, with narrow
upturned apex, with row of short setae on sternal
side distally.

Elamenopsis thorsbornei n. sp.
(Fig. 1)

MATERIAL EXAMINED
HOLOTYPE: Murray River, north of Cardwell,
North Queensland; 19.v.1978, P. Davie and P.
Shanco, ovigerous ♀ (4·8 mm, three walking legs
detached), sieved from sloppy mud at edge of
mangroves, north bank near mouth. (QM
W7804).

DIAGNOSIS
Carapace approximately ovate, dorsal surface
with four tubercles in cardiac region, no tubercles
in gastric region; lateral carapace walls without
spines; rostral lobes fused except for tridentate
terminal portion of three obtuse angles, medial
lobe projecting forward, lateral lobes longer and
broader than medial lobe, upturned distally;
carpus and propodus of 3rd and 4th walking legs
flattened and broad, propodus of 4th walking leg
about one quarter as broad as long.

DESCRIPTION
(Based only on female holotype). Carapace
width 4·8 mm, carapace length 5·1 mm (without
rostrum), 5·35 mm (with rostrum); dorsal
carapace surface finely granular, with convex
gastric, cardiac and branchial regions, cardiac
region with four tubercles, one tubercle each side
of midline and a smaller tubercle posterolateral to
it; rim of dorsal carapace surface elevated, except
across base of rostrum; anterolateral and
posterolateral carapace angles rounded obtuse and
little indicated; gastrocardiac, thoracic, cervical
and contiguous grooves well defined; branchio-
stegites sloping out slightly towards leg bases;
margin of rostrum with fine serrations; eyes short,
almost completely obscured in dorsal view by
carapace; postocular lobes small, acute; anten-
nules, when unflexed, reach to anterior of rostrum,
basal segment very stout with a strong
anterolateral lobe fringed with setae; interanten-
nular septum prominent, very broad at base,
extending forward beyond basal annular
segment to meet rostral keel; rostral keel
moderate, extending to base of medial rostral lobe;
antennal spines small, sited posterolateral to bases
of antennae; pterygostomial region with strong
dorsal ridge; mouth-frame with strong antero-
lateral ridge.
Third maxillipeds with strong setae along inner
edges of ischium and merus and arising from a
medial longitudinal ridge on ischium, ischium with
prominent anteromedial lobe, palp extending to
ischio-merus junction, exopodite conspicuous,
epipodite prominent in strongly arched Milne-
Edwards aperture; female chelipeds c. 6 mm long,

little stouter than walking legs, maximum depth of propodus 1·1 mm; fingers curved, meeting distally, each with five low teeth in gape; walking legs long, 2nd walking legs longer than 3 X carapace width, ischium and merus not flattened, merus with short terminal spine, carpus and propodus flattened and broadened, especially in 3rd and 4th walking legs, dactyli tapering to simple point, without teeth, dactyli more slender and curved on 1st and 2nd walking legs.

Abdominosternal region typical of *Elamenopsis* females, pleopods absent, eggs apparently brooded within abdomen and cephalothorax cavities, segment 2 of abdomen very short, segments 3–5 fused, telson also possibly fused (not clearly indicated); eggs c. 0·32 mm diameter; genital apertures subcircular, sited on sternum between bases of 1st walking legs.

Body coloured very light brown with brown stripes (alcohol preserved specimen), brown stripes extend laterally on each side of the dorsal carapace surface, meeting in the frontal and gastrocardiac regions in a somewhat A-shaped configuration, another brown stripe in midline of cardiac region, another brown stripe on each lateral carapace wall extending from eye along and above leg bases; setation minimal, present on mouthparts and antennules, scattered on chelipeds, and fringing abdomen.

DISTRIBUTION
Murray River, NE.Q.

REMARKS
E. thorsbornei is most closely related to the other *Elamenopsis* taxa with tubercles on the dorsal carapace surface, i.e. the *E. tuberculata* complex, *E. t. tuberculata* (Chopra and Das) from southern India, *E. t. attenuipes* (Chopra and Das) from southern India and *E. t. pageti* (Pretzmann) from Sri Lanka; these may be three species rather than three subspecies (Lucas, 1980). Apart from tubercles, these taxa share other important features: (i) rounded (not angular) carapace form; (ii) dactyli of walking legs without teeth; (iii) rostrum trilobate but short and with lateral lobes broader than the medial lobe; (iv) walking legs with compressed segments.

E. thorsbornei is readily distinguished from the *E. tuberculata* taxa in having no spines on the lateral carapace walls, no tubercle in the gastric region and a different pattern of tubercles in the cardiac region of the carapace, a rostrum with greater fusion of the lobes, and very unequal compression of the segments within each leg and between legs.

We suggest that the non-tuberculate species most closely related to *E. thorsbornei* and *E. tuberculata* are: *E. demeloi* (Kemp) which has all the above features (i–iv); *E. ariakensis* (Sakai) which has all the above features except possibly the walking legs which Sakai (1969) describes as "stout," and which may be compressed (see Sakai, 1969, text figure 2); and *E. frontalis* n. sp. which has all the above features except (ii), the absence of dentition on walking leg dactyli. This suggestion is contrary to Chopra and Das (1930) and Pretzmann (1975), who placed *E. tuberculata* with *E. woodmasoni* (Alcock), *E. alcocki* (Kemp) and *E. kempi* (Chopra and Das) on the basis of one character: presence of spines on the lateral carapace walls.

Two other species, *E. lineata* and *E.(?) palawanensis* Serene (see Lucas, 1980), have laterally compressed legs. They have quite different rostra to *E. thorsbornei* and differ from it in various other features, suggesting no close affinity.

E. thorsbornei may be unique among hymenosomatids in having a pattern of stripes on the carapace. The positioning of stripes on the holotype of *E. thorsbornei* suggests a regular pattern and it remains to be seen whether further collections confirm the stripes as characteristic of the species. Most hymenosomatids are a uniform cryptic colour and in the case of *Elamenopsis* species, which usually live on muddy substrates, the colour is usually dull brown. In one other *Elamenopsis* species, *E. introversa* (Kemp), two specimens were noted to have markings 'somewhat like a *fleur-de-lys*' (Kemp, 1917). Some *Halicarcinus* species are multi-coloured, but these have patches of colour of variable pattern rather than clear stripes.

The holotype was collected during an Australian Littoral Society/Queensland Museum survey of Murray River and this species is named after Arthur and Margaret Thorsborne who own a property near Murray River and who greatly assisted members of the survey.

Elamenopsis hirtirostris n. sp.
(Fig. 5a—e)

MATERIAL EXAMINED
HOLOTYPE: Daintree River, North Queensland, 13.ix.1976, R.G. Pearson and L.K. Penridge, ♂ (3·0 mm, one walking leg lost), collected in artificial substrate traps (QM W9096).
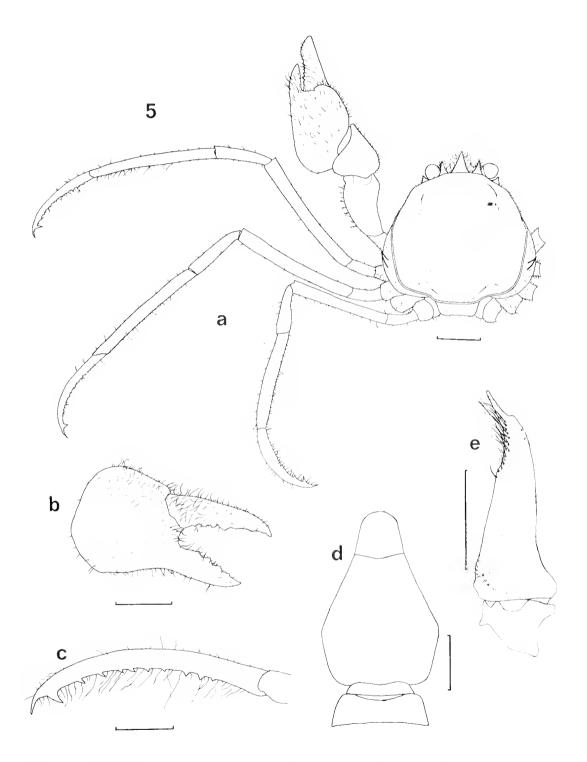
FIG. 5: *Elamenopsis hirtirostris* n. sp., Holotype, (a) dorsal view (b) left chela (c) dactylus of third walking leg (d) male abdomen (e) first male pleopod (lateral view of right side of right pleopod). Scales: a, b = 1 mm; c, d, e = 0·5 mm.

PARATYPES: Daintree River, North Queensland, 13.ix.1976, R.G. Pearson and L.K. Penridge, 3 ♀♀ (3·4–3·5 mm), collected in artificial substrate traps (QM W9097); Daintree River, North Queensland, 30.v.1977, R.G. Pearson and L.K. Penridge, ♂ (2·9 mm), benthic sample using net (QM W9098); Daintree River, 22.xi.1976, R.G. Pearson and L.K. Penridge, ovigerous ♀ (3·0 mm), 2 immature ♀♀ (1·3, 1·6 mm), juvenile (0·9 mm), collected in artificial substrate traps (JCU).

DIAGNOSIS

Carapace subcircular; lateral carapace walls with a spine below carapace rim, above base of 1st walking leg; rostrum consisting of three separate spine-like lobes, lobes fringed with setae which are longest and most dense on medial lobe, rostral region densely setose, lateral rostral lobes well spaced from medial lobe, pointing distinctly upward, medial lobe longest, pointing forward, arising distinctly below carapace rim; walking legs not laterally compressed, dactyli with a subterminal tooth and c. 8 recurved teeth spaced along ventral edge; male 1st pleopod with a distinct thin terminal portion tapering to a point, distal portion with row of setae on sternal side.

DESCRIPTION

Ratio of carapace width to carapace length (including rostrum) 0·93 (♀♀) and c. 1·00 (♂♂); dorsal carapace surface approximately flat, with gastric, cardiac and postbranchial regions convex; gastrocardiac, cervical and thoracic grooves well defined, contiguous grooves weak; branchiostegites sloping out slightly ·towards leg bases; anterolateral and posterolateral carapace angles rounded obtuse; rostral region densely setose with long setae arising from undersurface of medial rostral lobe and from carapace wall between rostral lobes, in addition to fringing setae on rostral lobes; eyes short, outreached anteriorly by lateral rostral lobes, cornea fully visible in dorsal view; postocular lobes small and acute; antennules longer than rostrum when unflexed, basal segment with acute lateral lobe bearing setae (adding to setation of rostral region); antenna with long flagellum; interantennular septum prominent, extending to base of medial rostral lobe; no rostral keel; no antennal spine; pterygostomial region with strong dorsal ridge.

Ischium and merus of 3rd maxilliped with strong setae along inner edges, ischium with distinct anteromedial lobe, palp stout, not reaching ischio-merus junction, exopodite and epipodite conspicuous; length of male chelipeds greater than 1·5 X carapace width, much stouter than walking legs, propodus especially inflated and expanded ventrally, merus with small tooth on ventral surface near outer–distal edge, fingers slightly curved, meeting distally, fingers each with c. 4 irregular teeth, chelipeds of holotype male quite setose, especially on dorsal margin of carpus, outer surface of propodus and fingers; length of female chelipeds c. 1·2 X carapace width, female chelipeds stouter than walking legs but much smaller and less setose than male chelipeds, fingers meeting along most of length, each with c. 4 low teeth; walking legs long and slender, length of 2nd walking leg almost 2·5 X (♀ ♀) to almost 3 X (holotype ♂) carapace width, dactyli slender and curved distally, with a subterminal tooth and c. 8 recurved teeth along ventral edge, walking legs setose, especially on ventral surface of propodus and dactylus.

Female abdominosternal region without pleopods, typical of *Elamenopsis* species, segments 1 and 2 short, segments 3–5 fused, making major part of abdomen, telson short, broad and arcuate; female genital apertures oval, with raised anterior rim, sited on sternum just posterior to bases of chelipeds; male abdomen with segments 1 and 2 short, fused article of segments 3–5 expanding to maximum abdomen width then tapering uniformly to telson, telson trapezoidal with rounded distal angles; male 1st pleopods little curved, moderately stout, with a distinct thin terminal portion tapering to a point, and projecting towards sternum, with a row of setae subterminally on sternal side and several small curved setae distally on abdominal side of pleopod.

Body colour light brown to brown (alcohol preserved specimens); body setose with short setae on dorsal carapace surface and long setae on lateral carapace walls, sternum, chelipeds, walking legs and abdomen; some plumulose setae around posterior of body, proximal segments of walking legs and outer surface of chelae of large male tending to accumulate silt particles and taking on a clubbed appearance; mature females 3·4–3·5 mm carapace width; males 2·9 and 3·0 mm carapace width with inflated chelae.

DISTRIBUTION

Daintree River, NE. Queensland.

REMARKS

E. hirtirostris belongs with the large group of *Elamenopsis* species which have a subcircular carapace, short tripartite rostrum of narrow lobes and long, unflattened legs. These species are

mutually distinguished by features such as the form of the rostral lobes and their degree of fusion, development of body spines, and armature of the walking leg dactyli. *E. hirtirostris* is most similar to *E. octagonalis* (Kemp). It is most clearly distinguished from *E. octagonalis* by its series of recurved teeth spaced along the walking leg dactyli; *E. octagonalis* has only a subterminal tooth and some serrations on the ventral surface of the dactylus in some specimens. (The row of teeth on the dactylus also distinguishes *E. hirtirostris* from the other similar *Elamenopsis* species reported from Australia, *E. aspinifera* Lucas and *E. torrensica* Lucas). Other features in which *E. hirtirostris* differs from *E. octagonalis* are: less angular carapace shape; rostral region more setose, with a tangle of setae rather than the regular fringing setae of *E. octagonalis;* spines on the lateral carapace walls not as long or projecting as vertically; terminal portion of male 1st pleopod thinner, more pointed and more distinct from shaft of pleopod (cf. Fig. 5e to Fig. 4) and greater setation, including presence of 'clubbed' setae.

The name *hirtirostris* (Latin, feminine) refers to the 'hairy' rostal region.

Elamenopsis minima n. sp.
(Fig. 2a–d)

MATERIAL EXAMINED
HOLOTYPE: Calliope River, SE.Q., July 1979, P. Saenger, ♀ (2·4 mm, specimen with only left cheliped and right walking leg 2 present, one detached walking leg with specimen), (QM W8848).

PARATYPES: Same locality as holotype; Feb. 1977, P. Saenger, 3 ♂ ♂, ovigerous ♀, immature ♀ (1·0 —1·7mm, all specimens without limbs, some detached walking legs and chelipeds present), (QM W8847); July, 1979, P. Saenger, 2 immature ♀ ♀ (1·6, 1·8 mm, larger specimen with only right cheliped attached, other specimen without limbs, some detached walking legs and cheliped present), (QM W8849).

DIAGNOSIS
Carapace approximately ovate; lateral carapace walls without spines; rostrum consisting of one long thin lobe, tip of rostrum rounded, often with two long and two very long forward projecting setae; walking legs not laterally compressed, dactyli with 2–7 recurved teeth along ventral edge; females mature at c. 2·0 mm carapace width.

DESCRIPTION
Ratio of carapace width to carapace length (including rostrum) 0·77–0·79 (♂ ♂), 0·80–0·84 (immature ♀ ♀), 0·85–0·86 (mature ♀ ♀); carapace width to length (excluding rostrum) ratio c. 1·0; dorsal carapace surface irregular, with convex gastric and cardiac regions; gastrocardiac, cervical and thoracic grooves strong, contiguous grooves weaker; lateral carapace walls sloping out to leg bases; carapace angles not indicated or posterolateral angles slightly indicated and rounded obtuse; rostrum arising well below carapace rim, moderately upturned with a row of well spaced setae along each lateral edge and ventrolaterally; eyestalks moderately long, tending to curve laterally, completely visible in dorsal view; postocular lobes prominent; antennules completely visible in dorsal view, basal segment long and stout and reaching to about half rostral length, basal segment with setae on distolateral edge, antennules terminating in two simple rami with a tuft of stout setae arising betwen rami (not from rami); antennae long; interantennular septum extending to base of rostrum; rostrum consisting of one long thin lobe, tip of rostrum rounded and often with two long and two very long setae arising from it and projecting forward, no rostral keel; no antennal spines; epistome short laterally, but longer medially due to projection forward between antennules and down into mouthfield.

Third maxilliped palp reaching ischio-merus junction, expodite prominent; female chelipeds stouter than walking legs but not much inflated, cheliped length c. 1·4 X carapace width, fingers curved distally, meeting along most of length with low serrations along cutting edges (no male specimens with chelipeds attached); legs slender, length of walking leg 2 of holotype 2·35 X carapace width, dactyli curved with longer recurved teeth distally.

Female abdominosternal region typical of *Elamenopsis* species, fused segments 3–5 constitute all of ventral portion of abdomen; telson small, rather transversely rhombic; eggs c. 0·25 mm diameter, c. 20 eggs visible in abdomen and cephalothorax of 1·7 mm ovigerous female; male abdomen with segments 1 and 2 short, article of fused segments 3–5 expanding to widest point of abdomen then tapering to telson, telson apparently fused with segments 3–5 with suture evident, telson rounded terminally; male 1st pleopods moderately stout and straight (see Remarks) distally tapering to a distinct thin terminal portion, with c. 5 setae distally along sternal edge and several short setae distally on abdominal edge.

Body coloured yellow to pale brown (alcohol preserved specimens); long setae scattered over body, most abundant on lateral and posterior carapace regions and on legs; mature females 1·7 and 2·4 mm, largest immature female 1·8 mm; largest male 1·3 mm.

DISTRIBUTION

Calliope River, Central Queensland.

REMARKS

Three other species of *Elamenopsis* have single lobed rostra. Two of these, *E. lineata* and *E. inermis* (Takeda and Miyake), have a short deflexed rostrum and in this and other morphological features they do not appear to be closely related to *E. minima*. The other species, *E. nasalis* (Kemp), has a similar rostrum to *E. minima* though shorter, and its atypical frontal region, with very exposed eyestalks and antennules, is also in common with *E. minima*. Other features which these species share are general carapace shape, slender uncompressed legs, absence of spines on lateral carapace walls and general setation. *E. minima* differs from *E. nasalis* in having a longer rostrum, long terminal setae on the rostrum, prominent postocular lobes, an interantennal septum, at least two teeth and often a row of teeth on the dactyli of walking legs, and a typical male abdomen. The male abdomen in *E. nasalis* is unusually broad, the fused article of segments 3–5 being broader than long, and there is a large tubercle distally. Since shape of the male abdomen reflects the form of the 1st pleopods it is quite possible that *E. nasalis* has atypical male 1st pleopods. Thóse of *E. minima* are quite typical of *Elamenopsis* males. The 1st pleopod illustrated in Fig. 2d is from a male which is considerably smaller than the largest female and may represent a fairly immature condition.

The ovigerous female paratype of *E. minima*, 1·7 mm carapace width, is the smaallest mature female reported for any hymenosomatid species and also probably the smallest mature female crab, free living or commensal, that has been reported. R.G. Hartnoll (pers. comm.) comments 'The only cases I can think of which might dispute the claim [that *E. minima* is the smallest crab species] are some of the very sexually dimorphic hapalocarcinids. The females are not as small, but the mature males are of the order of 1 mm.' Hymenosomatids in general are amongst the smallest brachyurans and there are species of *Elamena, Elamenopsis* and *Halicarcinus* which mature at less than 3 mm carapace width;

however, *Halicarcinus keijibabai* (Takeda and Miyake) is the only other species for which a mature female less than 2 mm carapace width has been found.

The name *minima* (Latin, feminine) refers to the very small size of this species.

Elamenopsis frontalis n. sp.
(Fig. 6)

MATERIAL EXAMINED

HOLOTYPE: North Mossman River, North Queensland; 25.v.1977, R.G. Pearson and L.K. Penridge, ♀ (3·4 mm, right cheliped and a walking leg lost), collected in an artificial substrate sampler (QM W9095).

DIAGNOSIS

Carapace oval, broader than long, ratio of carapace width to length (without rostrum) less than 1·2; frontal region distinguished by being somewhat extended forward; rostral lobes unfused, medial lobe small, triangular and not deflexed, lateral lobes very short and extending around curved edge of frontal region; merus of walking legs laterally compressed, dactylus with a strong subterminal tooth, walking legs with numerous long setae along ventral edges of segments from merus to dactylus.

DESCRIPTION

(Based only on female holotype). Ratio of carapace width to length 1·19 (with rostrum) and 1·14 (without rostrum), dorsal carapace surface with convex gastric, cardiac and branchial regions; carapace rim elevated; gastrocardiac, thoracic and cervical grooves deep, contiguous grooves extending to carapace rim, cardiac region strongly indicated by grooves; branchiostegites nearly vertical, bulging slightly; anterolateral angles rounded obtuse, well forward, posterolateral angles not indicated; rostral lobes fringed with setae; eyestalks short, somewhat bent laterally; postocular lobes with small points; antennules of moderate length, visible in dorsal view, basal segment with setose lateral lobe, peduncle of two segments; antenna with long flagellum; interantennular septum broad and strong, reaching rostrum; no rostral keel or antennal spines; pterygostomial region plain.

Third maxillipeds well separated medially, palp stout, barely reaching ischio-merus junction, expodite largely concealed; length of chelipeds c. 1·2 X carapace width, merus stouter than largest walking leg merus, propodus slightly inflated,

fingers meeting along length, with interlocking teeth, c.4 teeth per finger, fingers curved slightly distally; length of walking legs c. 1·8 X carapace width, legs moderately stout, laterally compressed, but not strongly so, lateral compression most evident in merus segment, dactylus tapering and curved distally without teeth other than subterminal tooth.

Female reproductive morphology typical of genus, abdominal segments 1 and 2 visible dorsally, fused article consisting of segments 3–5 and also telson which is not differentiated from abdomen, fused article approximately oval, broader than long with rounded point at telson; female genital apertures round, c. 0·15 mm diameter.

Body coloured very light brown (alcohol preserved specimen); quite setose, normal setation on mouth parts and Milne-Edwards apertures, rather plumulose setae in rostral region, at posterior and lateral edges of body and around leg bases, scattered setae on chelipeds, walking legs and abdomen, 2 approximate rows of setae on ventral edges of leg segments; mature female 3·4 mm carapace width.

DISTRIBUTION
North Mossman River, NE.Q.

REMARKS
The female holotype of *E. frontalis* is quite distinct from other Australian species of *Elamenopsis* and most like *E. ariakensis* Sakai, a Japanese species which is commensal with a species of holothurian. The rostra of *E. frontalis* and *E. ariakensis* are similar, although the lobes are not separated in the latter species. In *E. ariakensis* the carapace is broader (carapace width to length ratio c. 1·4) and the frontal region is not produced. The merus segments of walking legs are apparently more compressed in *E. ariakensis* than in *E. frontalis* and in the former the walking leg dactyli do not have any teeth. *E. frontalis* is distinguished from the other *Elamenopsis* species with compressed leg segments i.e. *E. lineata, E. demeloi, E. tuberculata, E. ariakensis and E. thorsbornei* by having subterminal teeth on its curved walking leg dactyli. *E.(?) palawanensis* Serene (see Lucus 1980) also has compressed leg segments however Serene's diagnosis and figure are inadequate for showing the presence or absence of subterminal teeth on the walking leg dactylus. It can be separated from *E. frontalis* by its much wider compressed walking legs and the unusually elongate lateral rostral lobes.

The name *frontalis* (Latin, feminine) refers to the prominent frontal region of the holotype.

Amarinus Lucas 1980
Amarinus paralacustris (Lucas 1970)
(Fig. 7)
Halicarcinus paralacustris Lucas 1970, p. 275–7, figs. 3c, e; 1971, p. 475–82, figs. 3JK, 5EFGH (larval morphology).
Amarinus paralacustris: Lucas 1980, p. 204–5, (part) figs. 4E, 7C, 10A (see Remarks).

MATERIAL EXAMINED
Calliope R., Central Queensland, 9–13. vii. 1976, P. Saenger, ♂ (4·0 mm), 2 immature ♀ ♀ (2·9, 4·2 mm), 14 km from mouth, edge of channel (QM W6812); Burnett R., SE.Q., 20.x.1980, R.G. Pearson and L.K. Penridge, 2 ovigerous ♀ ♀ (5·4, 6·4 mm) from hard substrate (JCU).

DIAGNOSIS
Rarely exceeding 10 mm carapace width; anterolateral carapace margins plain; rostrum meeting but not fused with postocular lobes; antennal spines obtuse and inconspicuous; female genital apertures 0·4–0·5 mm wide with a curved medial prominence; eggs c. 0·35 mm diameter; mean value of breadth/length ratios of inner rami of pleopods c. 0·4; telson length/total abdomen length c. 0·35 in mature females; male first pleopod very stout, tapering to a simple tip.
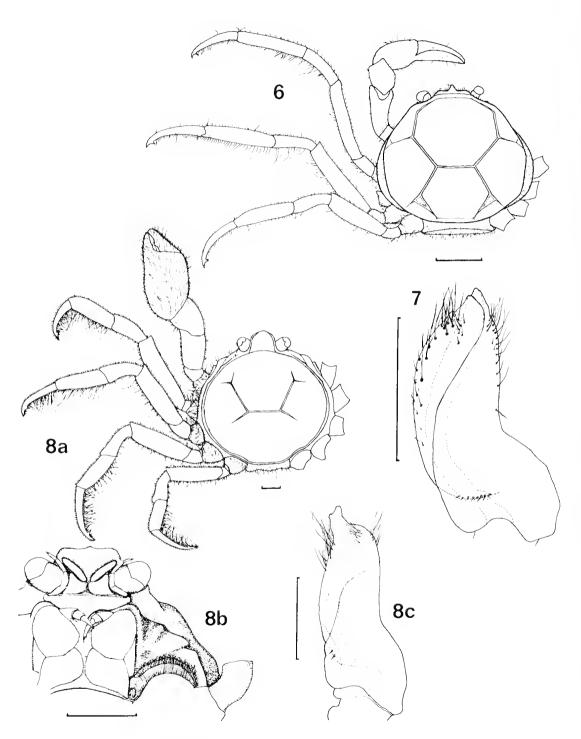
DISTRIBUTION
Temperate and subtropical eastern Australian mainland, in estuaries along the coast from Anglesea, Victoria, to Calliope R., Central Queensland.

REMARKS
The specimens of *Amarinus* from northern Queensland which Lucas (1980, p.205) provisionally identified as *A. paralacustris* while recognising that these specimens differed in some important respects from the southern specimens, are now recognised as being conspecific with the *A. latinasus* holotype. The most northern locality now known for *A. paralacustris* is Calliope River (24° 00' S) in Central Queensland i.e. *A. paralacustris* has a temperate-subtropical distribution in eastern Australia. *A. latinasus* is a tropical species, known from Herbert River (17° 30' S) and further north. The two species are distinguished by a number of features (Table 1) but most obviously by the female genital aperture and male 1st pleopod.

FIGS. 6–8: 6. *Elamenopsis frontalis* n. sp., dorsal view, Holotype; 7. *Amarinus paralacustris,* first male pleopod (lateral view of right side of right pleopod); 8. *A. latinasus* (a) dorsal view of female (b) pterygostomial region of female (c) first male pleopod. Scales: 6, 8a, b = 1 mm; 7, 8c = 0·5 mm.

The male specimen from Calliope River appears to be at its final instar, although quite small. Its 1st pleopod is figured (Fig. 7) to show the conformity with southern specimens (c.f. Lucas 1980, fig. 10A) and for comparison with the pleopod of *A. latinasus* and *A. lutarius* n. sp.

Amarinus latinasus Lucas 1980
(Fig. 8a–c)

Amarinus latinasus Lucas, 1980 (in part), p. 205–6. Figs. 7D, 9F (sec Remarks).

MATERIAL EXAMINED

HOLOTYPE: Johnstone River, NE. Queensland, 30.xi.1972, M. Draper, ♂ (2·0 mm, with abdomen and 1st pleopod detached and mounted on a slide), among *Elodea* at low salinity (QM W4066).

PARATYPES: collection details as for holotype, 3 ♂ ♂ (1·5, 1·7, 1·9 mm) (QM W9101).

OTHER MATERIAL: Herbert R., NE.Q., 1.vii.1975 — 10.xi.1976, R.G. Pearson, and L.K. Penridge, 4 ♂ ♂ (1·8–7·3 mm), 6 ovigerous ♀ ♀ (6·2–7·8 mm), 2 immature ♀ ♀ (2·4, 6·1 mm), juvenile (1·8 mm), from artificial substrate collectors and drift net (JCU, 7 lots); Herbert R., NE.Q., 3.iv.1976, R.G. Pearson and L.K. Penridge, ♂ (6·1 mm), ovigerous ♀ (6·5 mm), from artificial substrate collector (QM W9100); Murray R., NE.Q., 16.v.1978, R. Timmins, ♂ (4·1 mm), south bank opposite terrestrial patch, Tomahawk Bend, mid-estuary (QM W7802); Murray R., NE.Q., 24.v.1978, P. Davie, 2 immature ♀♀ (4·4, 5·5 mm), muddy-sand substrate, benthic grab sample (QM W7801); South Johnstone R., NE.Q., 28.ix.1976, 26.x.1977, R.G. Pearson and L.K. Penridge, ♂ (2·3 mm), 2 immature ♀ ♀ (2·2, 5·2 mm), dredge and benthic samples (JCU, 2 lots); North Johnstone R., NE.Q., 11.xi.1975, R.G. Pearson 4 ♂ ♂ (2·8–5·3 mm), 2 immature ♀ ♀ (2·2–4·8 mm), found in weedy backwater, near-fresh water, dredge sample, about 5 km from mouth (JCU); North Johnstone R., NE.Q., 26.ix 1976, R.G. Pearson and L.K. Penridge, ♂ (4·5 mm), collected by hand net (JCU); Russell R., NE.Q., 24.ix.1976–20.vi.1978, 16 ♂♂ (1·8–5·4 mm), ovigerous ♀ (4·9 mm), 6 immature ♀♀ (2·2–5·2 mm), dredge and benthic samples (JCU, 4 lots); North Mossman R., NE.Q., 19.xi.1976, R.G. Pearson and L.K. Penridge, ♂ (2·2 mm), benthic sample (JCU); Daintree R., NE.Q., 21.v.1976–30.v.1977, R.G. Pearson and L.K. Penridge, 3 ♂ ♂ (4·0–5·5 mm), juvenile (2·1 mm), benthic sample (JCU, 3 lots).

DIAGNOSIS

Lateral extensions of rostrum substantially fused with postocular lobes above eyestalks; postocular lobes prominent, developed into acute lobes below carapace rim, not extending back along anterolateral carapace borders; upper ridge of ptcrygostomial region with lobe near mouth frame in large specimens; male 1st pleopod stout, not tapering, with broad apical region projecting towards sternum; genital apertures of mature females oval without medial prominences; large mature females less than 10 mm carapace width. (Modifed from Lucas 1980.)

DESCRIPTION

The following is a redescription of this species necessitated by the removal of the female paratype from the type-series (see Remarks), and from examination of mature male and female specimens.

Carapace subcircular, ratio of carapace width to length (including rostrum) 0.88–1.00, greatest in large specimens; dorsal carapace surface flat to slightly convex, with gastro-cardiac, cervical and thoracic grooves, thoracic grooves short and angled quite laterally; antcrolateral angles obtuse, situated well forward, posterolateral angles not indicated; carapace rim often with a series of low vertical prominences, first prominence on anterolateral angle, second and largest prominence on mid-lateral border and up to six small prominences along latcral border; branchiostegites nearly vertical in small specimcns, sloping out ventrally near last walking legs in large specimens; rostrum spade-shaped, with rounded obtuse apex; eyes short; antennules largely concealed in dorsal view when flcxcd; interantennular septum narrow; rostral keel indistinct; antennal spines very small; epistome very short; upper ridgc of pterygostomial region prominent with distinct lobe near anterolateral edge of mouth frame in large specimens and prominences on either side of pterygostomial and branchiostegite junction anterior to cheliped bases; Milne-Edwards apertures normal.

Mouth field wider than long, almost completely filled by 3rd maxillipeds; ischium of 3rd maxillipeds shorter than merus along lateral edge, palp not reaching ischio-mcrus junction, exopodite largely concealed; length of male chelipeds c. 1.33 X carapace width, propodus inflated, without a ventral kccl, propodus with dense hairs on outer surface, fingers curved and gaping widely proximally, dactylus with basal tooth in gape, fingers meeting distally with small teeth on

cutting edges, fixed finger slightly angled downward compared to lower edge of palm; length of female chelipeds less than carapace width, propodus only slightly stouter than merus of largest walking leg; length of walking legs c. 1.5 X carapace width (♂♂), slightly greater than carapace width (mature ♀), legs moderately thick, dactyli distinctly more slender than propodi, dactyli little curved, with prominent subterminal tooth and two rows of ventral setae.

Female abdomen oval and convex with two prominent submedial grooves diverging proximally to give a prominent medial portion on segments 1 and 2 in dorsal view, segments 1–5 progressively longer and broader, telson arcuate, c. 0.4 total abdomen length; eggs c. 0.38 mm diameter; segments 1 and 2 of male abdomen shorter and broader than segments 3–5, segments 3–5 of similar length, tapering to telson, telson spade-shaped with broadly rounded apex; male 1st pleopods with small tuft of setae terminally on abdominal side and short setae near apex.

Body coloured light brown (alcohol preserved specimens); setae on mouth parts, Milne-Edwards aperture, walking legs, around edge of female abdomen and on outer side of male propodus; mature females 4.9–7.8 mm, males with inflated chelae 5.1–7.3 mm.

DISTRIBUTION

Northern Queensland, known from Herbert River to Daintree River.

REMARKS

The type-series of *A. latinasus* nominated by Lucas (1980) consisted of the holotype juvenile male and 3 other juvenile males from Johnstone River and an ovigerous female from Weipa. Re-examination of these types and of further specimens of *Amarinus* from northern Queensland has revealed that two species are present. The female specimen has been designated as one of the paratypes of *A. lutarius* n. sp. which is described later in this paper. The original description of *A. latinasus* included features of this female specimen and therefore it was necessary to redescribe the species, as above.

A mature male pleopod (Fig. 8c) has been figured for comparison with the immature holotype, previously figured (Lucas, 1980, fig. 10F).

Amarinus lutarius n. sp.
(Fig. 9a–e)

Amarinus latinasus Lucas, 1980 (in part), figs. 4F, 6G (see Remarks under *A. latinasus,* this paper).

MATERIAL EXAMINED

HOLOTYPE: Murray River, NE. Queensland. 22.v.1978, P. Davie and P. Shanco, ♂ (3·8 mm, right 1st pleopod detached and mounted on slide), seiving at mouth, in front of mangrove island, mud substrate (QM W7800).

PARATYPES: Collection details as for holotype, ovigerous ♀ (3·9 mm) (QM W9631); Murray River, NE.Q., 24.v.1978, P. Davie, 9 ♂ ♂ (1·0–2·6 mm), 4 immature ♀ ♀ (1·7–3·3 mm), 17 juveniles (c. 0·9 mm X), benthic samples (QM W7793–W7799); Herbert River, NE.Q., 2.ix.1976, R.G. Pearson and L.K. Penridge, ♂ (3·9 mm), sand wash (QM W9099); Russell River, NE.Q., 10.xi.1977, R.G. Pearson and L.K. Penridge, 4 ♂ ♂ (1·5–2·6 mm), 2 immature ♀ ♀ (2·8, 3·4 mm), benthic sample (JCU); Weipa, NW.Q., July 1972, W. McCormick, ovigerous ♀ (4·1 mm, all limbs detached), benthic zone in front of mangroves (QM W4065).

DIAGNOSIS

Lateral extensions of rostrum substantially fused with postocular lobes above eyestalks; postocular lobes prominent, level and continuous with carapace rim, extending back along anterolateral carapace borders, so forming a horizontal shield across front of carapace with weakly deflexed rostrum; lateral edges of Milne-Edwards apertures and pterygostomian-branchiostegite junctions far forward of cheliped bases; male 1st pleopod moderately stout, not tapering, with apical region projecting medially, crest-like lobe projecting laterally; genital apertures of mature females oval without medial prominences; mature females less than 5 mm carapace width.

DESCRIPTION

Carapace subcircular, ratio of carapace width to length (including rostrum) 0·90–0·96, greatest in immature female; dorsal carapace surface flat to slightly concave or slightly convex, with gastrocardiac, cervical and thoracic grooves, thoracic grooves short and angled quite laterally; anterolateral angles rounded obtuse, situated well forward, posterolateral angles not indicated; mid-lateral carapace borders slightly indented behind anterolateral angles; branchiostegites vertical; rostrum with obtuse apex in females and small males, apex more elongate and acute in largest male; eyes short; antennules concealed when flexed; interantennular septum thin; no rostral keel; antennal spines very small and obtuse; epistome very short; pterygostomial region

reduced, due to anterior extension of branchiostegite and anterior position of Milne-Edwards aperture, pterygostomian-branchiostegite junction prominent, sited medially between cheliped base and anterolateral edge of mouth frame; anterolateral edges of mouth frame developed into prominences.

Mouth field wider than long, almost completely filled by 3rd maxillipeds; ischium of 3rd maxillipeds shorter than merus along lateral edge, palp short, exopodite largely concealed; length of male cheliped c. 1·25 X carapace width, propodus not strongly inflated, long setae on outer surface, fingers with narrow gape proximally, cutting edges slightly curved without teeth except for clongate low tooth on dactylus in gape; length of female chelipeds subequal with carapace width, propodus little stouter than walking legs, fingers

slightly less than half total propodus length, cutting edges plain; length of walking legs c. 1·75 X carapace width (largest ♂) and c. 1·5 X carapace width (♀ ♀), moderately slender, dactyli slender and tapering, curved distally with subterminal recurved tooth, two rows of long hairs ventrally.

Female abdomen oval and convex, similar to *A. latinasus;* eggs c. 0·35 mm diameter; male abdomen similar to *A. latinasus* but broader distally, telson distinctly wider than long; male 1st pleopod with small tuft of setae subterminally on abdominal side, row of setae on sternal side.

Body coloured light brown (alcohol preserved specimens); setae on mouth parts, Milne-Edwards apertures, walking legs, chelipeds and around edge of female abdomen; mature females 3·9, 4·1 mm, largest male 3·9 mm.
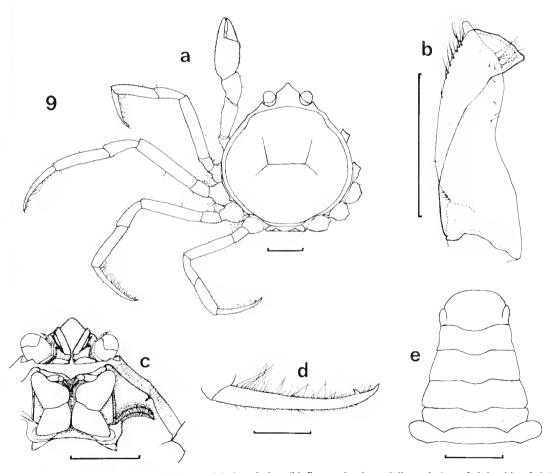
FIG. 9: *Amarinus lutarius* n. sp., Holotype (a) dorsal view (b) first male pleopod (lateral view of right side of right pleopod) (c) pterygostomial region (d) dactylus of third walking leg (e) male abdomen. Scales: a, c, d = 1 mm; b, d = 0·5 mm.

DISTRIBUTION

Northern Queensland, from Herbert River north.

REMARKS

A. lutarius has some unusual features which distinguish it from other *Amarinus* species: broad postocular lobes, reduced pterygostomial region and crested male 1st pleopod. It is most similar to *A. paralacustris* and *A. latinasus* and differences between these three species are summarised in Table 1. It is the smallest of the *Amarinus* species judging from the sizes of mature specimens so far collected.

A. lutarius and *A. latinasus* are both northern Queensland species and they are know to co-occur in three estuaries, the Herbert, Murray and Russell Rivers.

The name *lutarius* (mud dwelling; Latin, masculine) refers to the habitat of the type specimens.

Amarinus laevis (Targioni Tozzetti 1877)

Hymenosoma laeve Targioni Tozzetti, 1877, p.179–82, pl. 11 figs. 3a–e. (fig. 3d is incorrectly labelled 5d).

Amarinus laevis: Lucas, 1980, p.199–201, figs. 4C, 7A, 10D.

For full synonymy see Lucas, 1980.

MATERIAL EXAMINED

Corio Bay, north of Yeppoon, ME.Q., July 1974, R. Timmins, ♂ (12·8 mm), ovigerious ♀ (11·2 mm), (QM W4767). Mary River, S.E.Q., 17.x.81, N.L. Bruce and J. Fields, mud/gravel, c. 5–10 m depth, immature ♀ (6·4 mm) (QM W9745). Mary River, mouth of Tinana Ck., SE.Q., 15.x.81, N.L. Bruce, 2 ♂♂ (5·9, 6·9 mm) (QM W9746).

DIAGNOSIS

Mature specimens rarely less than 10 mm; males and females up to 22 mm and 18 mm respectively;

TABLE 1. MORPHOLOGICAL DIFFERENCES BETWEEN *AMARINUS PARALACUSTRIS, A. LATINASUS* AND *A. LUTARIUS* N. SP.

	A. paralacustris	*A. latinasus*	*A. lutarius* n. sp.
Thoracic grooves	typical	short, angled laterally	short, angled laterally
Lateral extensions of rostrum	meeting post-ocular lobes	fused with postocular lobes	fused with postocular lobes
Rostrum of large males	obtuse apex	obtuse apex	acute or near acute apex
Postocular lobes	acute lobe below carapace rim, not extended	acute lobe below carapace rim, not extended	level and continuous with carapace rim, extended along antlat. carapace borders
Mid-lateral carapace border	not indented	not indented, prominence	slightly indented behind antlat. angle
Pterygostomial region	plain	lobe near mouth frame	reduced
Milne-Edwards apertures	typical	typical	very anterior
Walking legs	moderately stout	moderately stout	more slender and slightly longer
Female genital apertures	with medial prominence	without medial prominence	without medial prominence
Male telson	length and width subequal	length and width subequal	length distinctly shorter than width
Male 1st pleopods	very stout, with terminal point	stout, with apex projecting towards sternum	moderately stout, with apex projecting medially and terminal crest
Carpus of male cheliped, ventral edge	with one or more large crenulations	without crenulations	without crenulations
Fixed finger of male cheliped, compared to ventral edge of propodus	angled distinctly downward	angled slightly downward	approximately parallel

anterolateral carapace margins without a row of teeth or thin spines; antennal spines acute and prominent; male 1st pleopod not tapering at apex, apex complex, with several lobes and tufts of setae; propodus of chela very deep in large males, with knife-edge ventrally and large pulvinus (a sac arising between the bases of the fingers).

DISTRIBUTION
Essentially a temperate species, stretching from Moore River in Western Australia around the southern coast, although penetrating subtropical Queensland waters to Corio Bay near Yeppoon, ME.Q.

REMARKS
Previously only known as far north as the Brisbane River, these records extend the known distribution considerably.

DISCUSSION
The known distributions of hymenosomatids in Queensland estuaries and tidal mud flats are summarised in Table 2. However, because the nineteen localities listed have not been sampled with equal intensity and because they represent only a small percentage of the suitable localities, the distributions indicated are only approximate. Species are listed in Table 2 according to latitudinal distribution and three patterns are evident:

1. temperate to subtropical species;
2. temperate to tropical species;
3. tropical species.

In the first category are four species, *Elamenopsis octagonalis*, *Amarinus laevis*, *Hymenosoma hodgkini* and *A. paralacustris*. The last three occur in estuaries and embayments all along the temperate eastern coast of mainland Australia, extending north into southern Queensland. *E. octagonalis* appears to be localised in distribution as it is only known in Queensland from Moreton Bay. This being the case, it is improbable that the Moreton Bay specimens are conspecific with the holotype from Mormugao Bay, India, the only other specimen reported. Lucas (1980) found only small differences between the Moreton Bay specimens and the holotype description of Kemp (1917) but was not prepared to give them separate taxonomic status on the basis of available morphological data.

TABLE 2: RECORDS OF HYMENOSOMATIDS FROM QUEENSLAND ESTUARIES AND TIDAL MUD FLATS. a — from Lucas (1980).

Species	COASTAL REGIONS AND LOCALITIES																		
	Southern		Central							Northern									Gulf
	Moreton Bay	Brisbane R.	Mary R.	Susan R.	Bogimbah Ck.	Burnett R.	Kolan R.	Calliope R.	Corio Bay	Ross R.	Herbert R.	Murray R.	Johnstone Rs.	Russell R.	Trinity Inlet	N. Mossman R.	Daintree R.	Thursday I.	Weipa
Elamenopsis octagonalis	X[a]																		
Amarinus laevis	X[a]	X[a]	X					X											
Hymenosoma hodgkini	X[a]					X	X	X											
Amarinus paralacustris		X[a]				X		X											
Halicarcinus bedfordi	X[a]			X	X	X		X		X[a]					X				X[a]
Elamenopsis lineata	X[a]							X		X		X			X				X[a]
Elamenopsis minima								X											
Elamenopsis aspinifera										X[a]		X							X[a]
Amarinus latinasus											X	X	X	X		X	X		
Amarinus lutarius											X	X		X					X
Elamenopsis thorsbornei												X							
Elamenopsis frontalis															X				
Elamenopsis hirtirostris																	X		
Elamenopsis torrensica																		X[a]	
Species Totals	5	2	1	1	1	3	1	5	1	3	2	5	1	2	2	2	2	1	4

In the second category, species occurring at all Queensland latitudes, are *Halicarcinus bedfordi* and *Elamenopsis lineata.* Their distributions extend beyond Queensland waters into Western Australia for the former species, and into northern New South Wales, New Caledonia and the Philippines for the latter species.

The remaining eight species make up the category of tropical species, with *Elamenopsis minima* being marginal. On present knowledge all are endemic to Queensland except for *E. torrensica,* the most northern species, which is known both from Torres Strait and Arnhem Land. Four species, *Amarinus latinasus, A. lutarius, E. torrensica* and *E. aspinifera,* have more or less extensive distributions while the other four *Elamenopsis* species are known only from single localities.

Although fourteen hymenosomatid species have now been reported from Queensland estuaries and adjacent localities, no more than five species have been collected from any one locality (Table 2). While recognising the geographical separation of temperate-subtropical and tropical species, this is only part of the explanation. The question arises as to whether the low numbers of species per locality reflect inadequate collecting or real differences in species complements at different localities? Inter-locality differences in species complements may result from:
1. different environmental conditions prevailing at those localities;
2. competition between species with broadly overlapping niche requirements;
3. limited capacities of some species to locate all suitable localities, which are discontinuous along the coast, or to recolonise localities where populations have been lost due to unfavourable conditions such as persistent low salinity — this limited capacity resulting from the low fecundity and limited larval dispersal characteristic of these species.

Unfortunately we know nothing about the habitat requirements of most of these hymenosomatid species, whether they have broad requirements or occupy quite specific niches, so it is not possible to assess the features of various localities in terms of their suitability for each hymenosomatid species.

In revising the family *Hymenosomatidae* Lucas (1980) recognised 64 species and this number is now raised to 69 with the descriptions of 5 new species in this paper. *Elamenopsis,* the largest of the ten hymenosomatid genera, is further enlarged and now contains 21 species. The genus *Amarinus* now contains eight species, five of them occurring in Australia. Because the Australian species of *Amarinus* are alike in general appearance, causing confusion in the past, and because of changes to the description of *A. latinasus,* a revised key for identification of the Australian species of *Amarinus* is provided here:

KEY TO AUSTRALIAN SPECIES OF *AMARINUS*

1. — Antennal spines acute and prominent; male 1st pleopod with complex apex of lobes, without a point; chela of large males with pulvinus (a sac arising between bases of fingers); mature females usually greater than 10 mm carapace width .... *A. laevis*
— Antennal spines obtuse and inconspicuous; male 1st pleopod with simple pointed apex; chela of large males without pulvinus; mature females usually less than 10 mm carapace width 2

2(1). — Rostrum little deflexed, apex acute or near acute in large males; postocular lobes level and continuous with carapace rim, extending back along anterolateral carapace border, not developed into a tooth; pterygostomial region reduced by anterior position of Milne-Edwards apertures; pterygostomial-branchiostegite junction approximately medial to cheliped base and anterolateral edge of mouth-frame; male 1st pleopod with apical crest ....*A. lutarius*
— Rostrum moderately deflexed, apex obtuse in large males; postocular lobe developed into a tooth below carapace rim, not extending back along anterolateral carapace border; pterygostomial region not reduced; pterygostomial-branchiostegite junction near cheliped base or nearer to cheliped base than edge of mouth-frame; male 1st pleopod without crest 3

3(2) — Pterygostomial ridge with small lobe near anterolateral edge of mouth-frame in large specimens; thoracic grooves on dorsal carapace angled strongly laterally, each forming a right angle or slightly obtuse angle with adjacent cervical groove; male 1st pleopod with apex on sternal side and pointing towards sternum; female genital apertures without a curved medial prominence ....*A. latinasus*
— Pterygostomial ridge without lobe near mouth-frame; thoracic grooves on dorsal carapace angled moderately laterally, each forming a distinctly obtuse angle with adjacent cervical groove; male 1st pleopod with terminal apex; female genital apertures

with or without a curved medial prominence
....4

4(3) — Female genital apertures 0·4–0·5 mm
wide, with a curved medial prominence;
eggs c. 0·35 mm diameter; telson c. 0·35 of
total abdomen length in mature females
.... *A. paralacustris*
— Female genital apertures 0·65 – 0·8 mm
wide, without a curved medial prominence;
eggs c. 0·7 mm diameter; telson c. 0·25 of
total abdomen length in mature females
....*A. lacustris*

ACKNOWLEDGEMENTS

LITERATURE CITED

CHALOUPKA, M.Y., 1978. 'An ecological study of
the decapod crustacean larvae in a tropical
estuarine embayment.' Unpublished Honours
thesis, James Cook University of North
Queensland.

CHOPRA, B. & K.N. DAS, 1930. Further notes of
Crustacea Decapoda in the Indian Museum. I.
On two new species of hymenosomatid crabs,
with notes on some other species. *Rec. Indian
Mus.* **32**: 413–29.

DESMAREST, A.G., 1825. 'Considerations Gener-
ales sur la Classe des Crustaces, et
Description des Especes de ces Animaux, qui
Vivent dans la Mer, sur les Cotes, on dans les
Eaux-Couces de la France . . .' Paris and
Strasbourg, XIX, 1–446, 5 tabs., pls. 1–56.

KEMP, S., 1917. Notes on Crustacea Decapoda in
the Indian Museum. X. Hymenosomatidae.
Rec. Indian Mus. **13**: 243–79.

KENWAY, M.J., 1980. 'Biological studies of
Callianassa australiensis (Dana).' Unpub-
lished Honours Thesis, James Cook Universi-
ty of North Queensland.

LUCAS, J.S., 1970. Breeding experiments to
distinguish two sibling species of *Halicarcinus*
(Crustacea, Brachyura). *J. Zool.* **160**(2):
267–78.

1971. The larval stages of some Australian

species of *Halicarcinus* (Crustacea, Brach-
yura, Hymenosomatidae). I. Morphology.
Bull. mar. Sci. **21**(2): 471–90.

1980. Spider crabs of the family Hymenosoma-
tidae (Crustacea; Brachyura) with particular
reference to Australian species; systematics
and biology. *Rec. Aust. Mus.* **33**(4): 148–247.

MACLEAY, W.A., 1838. Invertebratae. Vol. 2:
1–75, 4 pls. *In* A. Smith, 'Illustrations of the
Zoology of South Africa'. 5 vols (London:
Smith, Elder).

MELROSE, M.J., 1975. The Marine Fauna of New
Zealand: Family Hymenosomatidae (Crus-
tacea, Decapoda, Brachyura). *Mem. N.Z.
oceanogr. Inst.* **34**: 1–123, 2 pls.

MILNE-EDWARDS, A., 1873. Recherches sur la
Faune Carcinologique de la Nouvel-
le-Caledonie. *Nouv. Arch. Mus. Hist. nat.,
Paris* **9**: 155–332, pls. 4–18.

MONTGOMERY, S.K., 1921. Some Hymeno-
somidae from the Swan River. *J.R. Soc. W.
Aust.* **6**(2): 93–6.

1931. Report on the Crustacea Brachyura of the
Percy Sladen Expedition to the Abrolhos
Islands under the leadership of Professor W.J.
Dakin in 1913; along with other crabs from
Western Australia. *J. Linn. Soc. (Zool.)*
37(253): 405–65, pls. 24–30.

PRETZMANN, G., 1975. Brachyura aus Ceylon.
Annln naturh. Mus. Wien **79**: 605–8, pl. 1.

SAKAI, T., 1938. 'Studies on the Crabs of Japan.
III. Brachygnatha, Oxyrhyncha'. (Tokyo:
Yokendo Co.) 193–364, 22 pls.

1969. Two new genera and twenty-two new
species of crabs from Japan. *Proc. Biol. Soc.
Wash.* **82**: 243–80.

SERENE, R. and A.F. UMALI, 1970. The family
Raninidae and other new and rare species of
brachyuran decapods from the Philippines
and adjacent region. *Philip. J. Sci.* **99**(1/2):
21–105.

TARGIONI TOZZETTI, A., 1877. Zoologia del
Viaggio Intorno al Globo della R. Pirocorvet-
ta Magenta durante gli Anni 1865–68.
Crostacei Brachiuri e Anomuri. Pubbl. Inst.
Studi sup. prat. Firenze, Sezione di scienze
fisiche e naturalia 1:i–xxix, 1–257, 13 pls.

TESCH, T.T., 1918. The Decapoda Brachyura of
the Siboga Expedition. I. Hymenosomidae,
Retroplumidae, Ocypodidae, Grapsidae and
Gecarcinidae. *Siboga Exped.* **39**c(82): 1–148,
6 pls.

WHITE, A., 1846. Notes on four new genera of
Crustacea. *Ann. Mag. Nat. Hist.,* (1), **18**:
176–78.

NEW EUBRANCHIATE SPHAEROMATID ISOPODS FROM QUEENSLAND WATERS

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ABSTRACT

A number of new eubranchiate sphaeromatid isopods are described from the mainland coast and offshore islands of Queensland. *Neonaesa rugosa*, gen. nov., sp. nov. and *Pseudocerceis furculata*, gen. nov., sp. nov. are recorded from a number of coral reefs, whilst *Pistorius bidens*, gen. nov., sp. nov. occurs in beach rock crevices on Heron Island. The genus *Cerceis* Milne-Edwards is represented by three species, two being new, which occur on littoral and sub-littoral algae and amongst coral rubble. *Paradynamene benjamensis* Richardson has been synonymised with *Cerceis bidentata* var. *aspericaudata* Miers, which in turn has been raised to full specific status as *C. aspericaudata*. *Haswellia carnea* (Haswell) is recorded from Queensland for the first time, as is *Paracerceis sculpta* (Holmes). This latter record is the first time *P. sculpta* has been recorded in Australia.

INTRODUCTION

The marine isopod fauna of Queensland is very diverse and isopods are common in some habitats (Holdich and Harrison, 1980a, b, c; 1981a, b; Holdich *et al.*, 1981; Harrison and Holdich, 1982). This is especially true for eubranchiate sphaeromatids in the littoral zone, with species of *Sphaeromopsis* Holdich and Jones and *Dynamenella* Hansen being common in sandy habitats, and *Paradella* Harrison and Holdich and *Dynamenella* species being common in rock crevices and empty barnacle tests (Holdich and Harrison, 1981b; Harrison and Holdich, 1982). *Dynamene curalii* Holdich and Harrison has been found inhabiting intertidal and sublittoral coral (Holdich and Harrison, 1980c), and a species of *Ischyromene* Racovitza has been recorded from southern Queensland (Harrison and Holdich, 1982). Nine additional species of eubranchiate Sphaeromatidae have been recognized from Queensland, and these are described in the present paper. The collecting methods are as described in Harrison and Holdich (1982). The following abbreviations are used below: SEQ, South East Queensland; QM Queensland Museum; AM Australian Museum. The codes following QM or AM are the registered numbers of the specimens in those museums. Any specimen not allocated a museum registration number has been placed in a collection in the Department of Zoology at the University of Nottingham.

SYSTEMATICS

Order Isopoda

Family Sphaeromatidae

Sub-family Dynameninae

NEONAESA, gen. nov.

GENERIC DIAGNOSIS

Eubranchiate Sphaeromatidae with antennular peduncle article 1 not extended anteriorly as a plate. Both sexes with pereon and pleon lacking processes. Pleon with posterior margins bearing two short, weak, sutures at each side. Exopod of pleopod 5 bearing a large apical squamose boss and two smaller, internal squamose bosses. Lateral margins of pleotelson extending ventrally well beyond level of pereonal margins. Uropodal rami not lamellar, exopod extending beyond the highly reduced endopod. Sexual dimorphism obvious. **Adult male** with penes short, widely separate. Appendix masculina short, arising in distal half of

endopod of pleopod 2. Pleotelson apex with a wide, shallow indentation completely filled by a broad lobe bearing a short median slit. Uropod with exopod thick, longer than that of female, tapering distally. Maxillipcdal palp articlcs 2 to 4 bearing long, setigerous lobes. **Ovigerous female** with mouthparts strongly metamorphosed. Brood pouch formed from four pairs of oostegites arising from pereopods 1 to 4, increasing in size posteriorly and overlapping well in mid-line. Ventral pockets and pouches absent, but brood displaces sternites to fill cephalosome, pereon and pleon. Apex of pleotelson slightly extended with a vertical notch. Exopod of uropod shorter than that of adult male, narrow, terete.

ETMYOLOGY: *Neonaesa,* from the Greek *neos* meaning 'new', + *Naesa* (feminine). (*Naesa* being the name given to specimens of male *Dynamene* Leach in the past (see Holdich, 1968)).

TYPE SPECIES: *Neonaesa rugosa,* sp. nov.

ADDITIONAL SPECIES: none.

REMARKS

This genus bears some resemblance to the genus *Dynamene* but male specimens lack dorsal processes and have a lobed pleotelsonic apex, not an enclosed terminal foramen. They also possess an appendix masculina, do not have peduncle article 2 of the antennule acutely extended, and have the uropodal endopod greatly reduced. Ovigerous female specimens of *Neonaesa* differ from thosc of *Dynamene* by having a simple pleotelsonic notch, not an enclosed foramen; peduncle article 2 of the antcnnule simple, not acutely extended; the uropodal endopod reduced; the maxillipedal endite and palp less reduced; and by having the maxilla clearly lobed. *Neonaesa* does not closely resemble any other eubranchiate genus.

NEONAESA RUGOSA, sp. nov.

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum QM W7956, adult male, 2·3 mm, from intertidal reef flat, Heron Island, Queensland (23°25'S, 151°55'E), N.L. Bruce, 8 January 1979.

PARATYPES: QM W7958, ovigerous female, subadult male, immature specimen, same data as Holotype. QM W8046, W8049, W8052, W8053, W8056, W8058, W8062–67, W8069–71, W8073, 216 adult males, 22 subadult males, 69 ovigerous females, 51 immature specimens and non-ovigerous females, 27 juveniles, from inner reef flat, dead coral, intertidal, Heron Island, SEQ, N.L. Bruce, 23–30 May 1978 and 28 December 1978 to 15 January 1979. QM W8583, W8585–86, 23 adult males, 5 subadult males, 4 ovigerous females, 3 immature specimens, lagoon and 'Canyons', depth 3 to 7 m, Heron Island, SEQ, N.L. Bruce, 27 November 1979 to 8 December 1979. QM W8576, W8580–81, 22 adult males, 5 subadult males, 7 ovigcrous females, 1 immature specimen, 1 juvenile, southwest edge, east face and reef slope, depth 11 to 21 m, Wistari Reef, Capricorn Group, N.L. Bruce, 30 November 1979 to 4 December 1979. Australian Museum AM P26994, adult malc, ovigerous female, in coral reef rocks, west side of Palfrey Island (off Lizard Island), P. Hutchings and P. Weate, 12 January 1976. AM P26972–85, 21 adult males, 5 subadult males, 4 ovigerous females, 4 immature specimens, lagoon drop off, in coral rocks, depth 7·7 m, Lizard Island, Queensland (14°40'S, 145°30'E), P. Hutchings and P. Weate, 16 January 1976 to 6 November 1976. AM P26986–93, 5 adult males, 1 subadult male, 3 immature specimens, coral reef rocks, depth 3·7 m, Chinaman's Head, Lizard Island, P. Hutchings and P. Weate, 17 January 1976 to 7 November 1976. AM P26051, adult male, coral reef rock, depth 6 m, reef off North Point, Coconut Beach, Lizard Island, P. Hutchings and P. Weate, 17 January, 1975. AM P26058–9, 2 adult males, coral reef rocks, northeast face, Lizard Island, P. Hutchings and P. Weate, 6 January 1975. AM P28827, P28837, P28842, 3 immature specimens, Lizard Island. AM P26004–9, P26030, P26037, 7 adult males, immature specimen, on coral reef rocks, depth 2 to 5 m, back reef of Yonge Reef, P. Hutchings and P. Weate, 7 February 1975. AM P26015, P26020, P26026, 2 adult males, immature specimen, on coral reef rocks, depth 13 to 27 m, outer reef of Yonge Reef, P. Hutchings and P. Weate, 10–19 January 1975. QM W8078, subadult male, reef crest, in coral rock, North Cay, Chesterfield Reefs, Coral Sea (19°48'S, 158°17'E), N.L. Bruce, May 1979. Heron Island, inner reef flat, intertidal dead coral, 3 adult males, D.M. Holdich, 8–11 April 1976. Heron Island, reef flats on brown algae from live coral, immature specimen, G. Hartmann, 3 February, 1976. North Reef, Capricorn Group, lagoon 8 adult males, 1 subadult male, immature specimen, juvenile, N.L. Bruce, 7 June 1978. Lodestone Reef, Great Barrier Reef, dead coral, 7 adult males, 8 subadult males, ovigerous female, 7 immature specimens, 2 juveniles, T. Pearson,
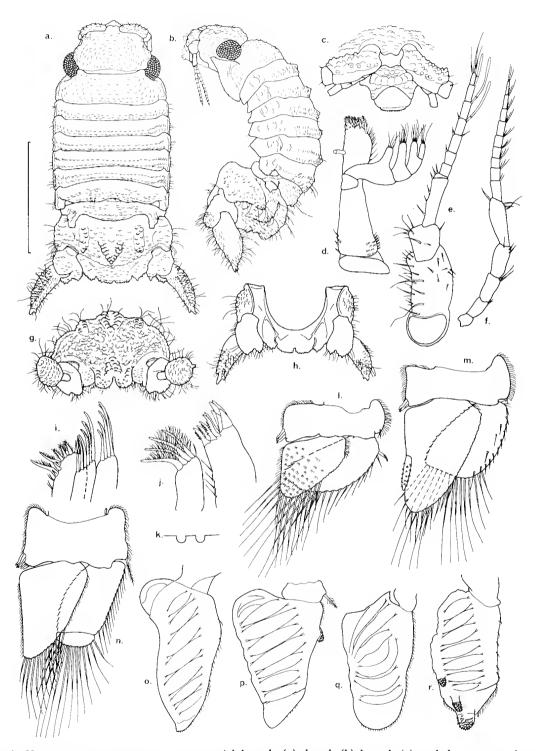
FIG. 1. *Neonaesa rugosa*, gen. nov., sp. nov. Adult male (a) dorsal, (b) lateral, (c) cephalosome, anterior, (d) maxilliped, (e) antennule, ventral, (f) antenna, (g) pleotelson, posterior, (h) pleotelson, ventral, (i) maxilla, (j) maxillule, (k) penes, (1–n) pleopods 1 to 3 respectively, (o) pleopod 4, endopod, (p) pleopod 4, exopod, (q) pleopod 5, endopod, (r) pleopod 5, exopod. Scale line represents 1 mm.
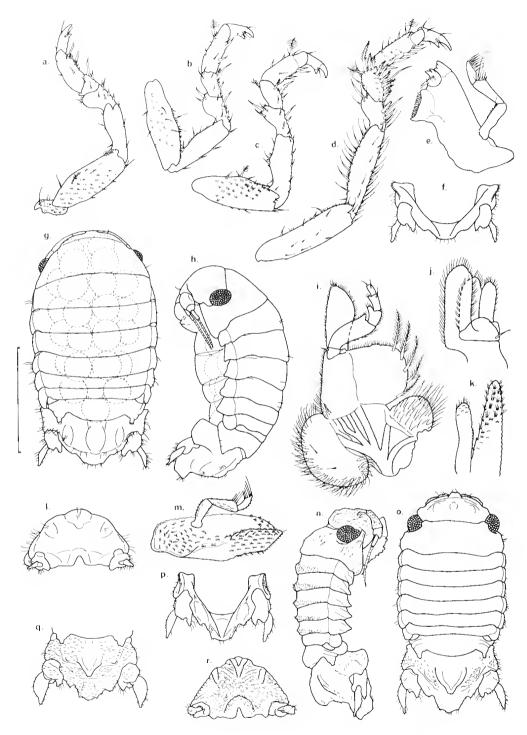
FIG. 2. *Neonaesa rugosa*, gen. nov., sp. nov. Adult male (a–d) pereopods 1, 2, 4 and 7 respectively, (e) left mandible. Ovigerous female (f) pleotelson, ventral, (g) dorsal, (h) lateral, (i) maxilliped, (j) maxilla, (i) maxillule, (l) pleotelson, posterior, (m) mandible. Non-ovigerous female (n) lateral, (o) dorsal, (p) pleotelson, ventral, (r) pleotelson, posterior. Subadult male (q) pleotelson. Scale represents 1 mm.

August 1976, Mellish Reef, lagoon, on dead coral, depth 6 m, immature specimen, N.L. Bruce, 1 May 1979.

DESCRIPTION

ADULT MALE: (Figs 1, 2a–e). Dorsal surface of body granular. Eyes large, lateral. Epistome with an uneven, transverse ridge. Coxal plates with lateral margins acute. Pleotelson with three uneven, longitudinal ridges, the central being broad anteriorly and tapering to an acute, raised point posteriorly. Posterior margin of pleotelson with three indentations — giving the impression of a broad notch completely filled by a bi-lobed expansion. Dorsal surface of pleotelson, anterior to the median notch, with slight longitudinal ridge.

APPENDAGES: antennule with article 1 of peduncle superiorly tuberculate, not bearing long, acute, distal extensions; article 2 subquadrate; article 3 slender; 8-articled flagellum extending to level of pereonite 2. Antenna subequal in length to antennule with 9-articled flagellum. Mouthparts of usual sphaeromatid form, unmodified; maxillipedal palp articles 2 to 4 bearing pronounced setigerous lobes. Pereopods moderately slender; merus, carpus and propodus bearing long inferior spines. Ischium of each of the posterior pereopods bearing superior and inferior setae. Penes widely separate, each as long as broad with a semi-circular tip. Basis of pleopod 1 with three internal coupling hooks; anterior surface of endopod bearing numerous microtrichia. Pleopod 2 with exopod truncate, shorter than subtriangular endopod; posterior surfaces of both rami bearing microtrichia (not illustrated). Appendix masculina short, cigar-shaped, bearing microtrichia, arising mid-way along internal margin of endopod and extending half-way to ramal apex. Exopod of pleopod 3 with a complete, subterminal articulation. Exopod of pleopod 5 with a subterminal, external, partial articulation. Uropod with endopod bearing an apical notch; exopod thick, granular, expanded dorsoventrally with an acute apex extending well beyond pleotelsonic apex.

COLOUR OF SPECIMENS IN ALCOHOL: cream, most specimens with very small black chromatophores sparsely distributed over dorsal surface. In life specimens are usually red in colour.

OVIGEROUS FEMALE, 2·2 mm: (Fig. 2f–m). Dorsal surface of body smooth. Cephalosome blunt, smoothly rounded. Pereon markedly domed; ova (when present) visible through dorsal body wall. Pleotelson with three low, longitudinal ridges; apex extended, with a simple lambdoid notch. Uropodal endopod narrow with an external notch; exopod just longer than endopod, narrow, cylindrical, tapering to an acute tip. Mouthparts strongly metamorphosed; mandible partially fused to cephalosome, tip angular with a longitudinal ridge; maxillule with two long, simple lobes; maxilla with three simple lobes; maxilliped with palp reduced, endite expanded proximally as three setose lobes.

NON-OVIGEROUS FEMALE: (Fig. 2n–p, r). Body finely granular (especially obvious in lateral view). Cephalosome with three weak ridges. Pleotelson with a prominent, central, posteriorly tapering boss, and a weak lateral ridge on each side. Apex extended with a simple lamboid notch. Uropods as in ovigerous female.

SUBADULT MALE: (Fig. 2q). As non-ovigerous female, but exopod of uropod dilated. No obvious penes. Appendix masculina not separate from endopod of pleopod 2, but visible beneath cuticle, partially separated from the endopodal tissue by a suture.

ETYMOLOGY: *Rugosa,* from the Latin *Rugosus* meaning wrinkled.

ECOLOGY AND DISTRIBUTION

This species is known from coral habitats on the offshore islands and reefs along the Queensland coast. It appears to be one of the commonest isopods in this region, occurring both intertidally and sublittorally. Its life style may be similar to that of *Dynamene curalii*, which also occupies coral habitats in Queensland. Both species are strongly sexually dimorphic, and the ovigerous females have reduced mouthparts. As with *D. curalii* juveniles and young adults probably feed on algae associated with corals whilst the mature adults take up a more cryptozoic existence for the reproductive phase of the life-cycle.

REMARKS

In dorsal view *N. rugosa* resembles *Geocereis barbarae* Menzies and Glynn, 1968 but *Geocerceis* has the sutures of the pleon reaching the lateral margins; the pleotelson lacking a central boss; pleopod 2 of the adult male of a very different form; and the pleotelson and uropods of females of different form.

Cassidias africana Barnard bears some resemblances to *N. rugosa* but in the adult male the pleotelson bears only one very extended process and the appendix masculina extends well beyond the apex of the pleopodal endopod. The brood pouch of *C. africana* is formed by three pairs of oostegites arising from pereopods 2, 3 and 4, but the brood is housed in internal pouches (K. Harrison pers. obsv.).
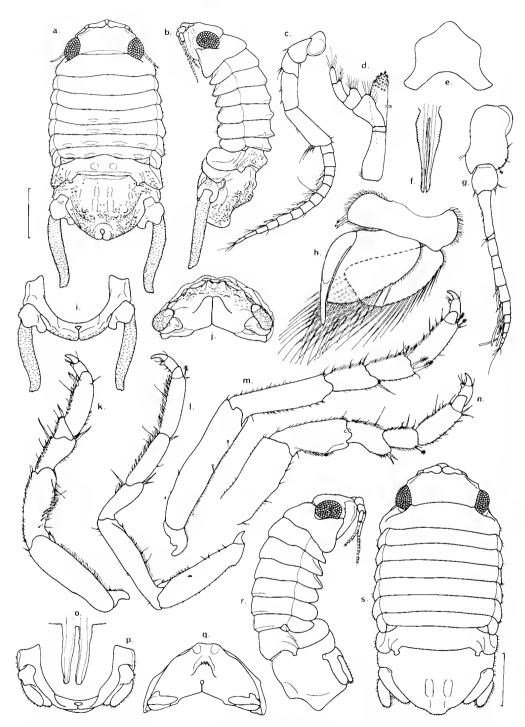
FIG. 3. *Pistorius bidens,* gen. nov., sp. nov. Adult male (a) dorsal, (b) lateral, (c) antenna, (d) maxilliped, (e) epistome, (f) penes, (g) antennule, (h) pleopod 2, (i) pleotelson, ventral, (j) pleotelson, posterior, (k–n) pereopods 1, 2, 7 and 4 respectively. Subadult male (o) penes. Ovigerous female (p) pleotelson. ventral, (q) posterior, (r) lateral, (s) dorsal. Each scale line represents 1 mm.

PISTORIUS, gen. nov.

GENERIC DIAGNOSIS

Eubranchiate Sphaeromatidae with antennular peduncle article 1 not extended anteriorly as a plate. Both sexes with pereon and pleon lacking processes. Pleon with posterior margin bearing two short sutures at each side. Maxillipedal palp articles 2 to 4 bearing weak, setigerous lobes. Exopod of pleopod 5 with a low apical boss, an extended subapical boss and a low internal boss. Lateral margins of pleon and pleotelson extending ventrally well beyond level of pereonal margins. Sexual dimorphism obvious. **Adult male** with penes long, tapering, fused at base. Appendix masculina arising from internoproximal angle of endopod of pleopod 2 and extending beyond ramal apex. Pleotelsonic apex with an enclosed, dorsally directed foramen. Uropodal endopod reduced; exopod subcylindrical, extending well beyond pleotelsonic apex. **Ovigerous female** with mouthparts not metamorphosed. Brood pouch lacking oostegites, formed from two opposing ventral pockets covering the entire ventral pereon and opening in the midline between the fourth pereopods. Apex of pleotelson with a tall vertical face bearing a posteriorly directed foramen connected to the ventral margin by a closed slit. Uropodal rami lamellar, narrow, subequal.

ETYMOLOGY: *Pistorius,* from the Latin *pistor,* meaning 'baker' + the ending *-ius* (masculine). (Named in honour of W.H. Baker).

TYPE SPECIES: *Pistorius bidens,* sp. nov.

ADDITIONAL SPECIES: none.

REMARKS

This genus resembles species of *Dynamenella* but differs in the form of the adult male uropods which have subequal, flattened rami in *Dynamenella,* and in the deep posterior closure of the pleotelsonic foramen. The type species *P. bidens,* sp. nov. is larger than species of *Dynamenella* (see Harrison and Holdich, 1982).

PISTORIUS BIDENS, sp. nov.

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum QM W7962, adult male, 4·35 mm, under slabs of beach rock intertidal (high water neap level), Heron Island, SEQ, N.L. Bruce, 8 December, 1979.

PARATYPES: QM W7963, ovigerous female, data as for holotype. QM W8584, 10 adult males, subadult male, 12 ovigerous females, non-ovigerous female, 2 juveniles, data as for holotype. Heron Island, beach rock crevice, upper shore, subadult male, 2 ovigerous females, non-ovigerous female, D.M. Holdich, 14 April 1976.

DESCRIPTION

ADULT MALE: (Figs 3a–n, 4). Dorsal surface of cephalosome and pereon smooth. Eyes large, lateral. Epistome short, tip narrowly rounded. Pereonal tergites 4 to 7 each bearing a transverse posterior ridge. Pleon granulose, bearing a low tubercle either side of midline. Pleotelson granulose with two elongate tubercles either side of midline forming irregular longitudinal ridges, and three separate tubercles lateral to each ridge. Apex of pleotelson with a small, elliptical, dorsally-directed foramen, enclosed posteriorly by a long vertical slit.

APPENDAGES: antennular peduncle article 1 as long as 2 and 3 together, not bearing long, acute, distal extensions; article 2 subquadrate, article 3 slender; 11-articled flagellum extending to level of pereonite 1. Antenna slender, 13-articled flagellum extending to level of pereonite 2. Mouthparts of usual sphaeromatid form, unmodified; maxillipedal palp articles 2 to 4 bearing low setigerous lobes. Pereopods moderately slender; merus, carpus and propodus bearing inferior pads of fine setae, and several long setae; superior surface of ischium with short fine setae. Propodus of pereopod 1 with a stout, inferodistal, pectinate spine; carpus also with one stout inferodistal spine. Penes broad proximally, tapering distally to narrowly rounded tips; margins crenulate in proximal half. Basis of pleopod 1 with three internal coupling hooks; endopod subtrapezial, extending just beyond elliptical exopod. Pleopod 2 with exopod truncate, just shorter than subtriangular endopod. Appendix masculina 1·3 times length of endopod, broad proximally, tapering evenly to a narrowly rounded tip. Exopod of pleopod 3 lacking an articulation. Exopod of pleopod 4 with a partial subterminal external articulation. Exopod of pleopod 5 with a complete subterminal articulation. Uropod with endopod strongly reduced, narrow, subquadrate; exopod long, sinuous subcylindrical, granulose, with apex slightly indented.

COLOUR OF SPECIMENS IN ALCOHOL: cream or red-brown with black chromatophores scattered over entire dorsal surface. Chromatophores may be expanded, giving a grey mottled appearance, or contracted as small black spots.

OVIGEROUS FEMALE, 4·6 mm: (Fig. 3p–s). Dorsal surface of body smooth. Pleotelson with a weak, low ridge either side of midline. Apex of pleotelson with a deep, flat, posteriorly directed face bearing a small foramen connected to ventral margin by a slit. Uropodal rami subequal, lamellar, with rounded apices not reaching apex of pleotelson.

NON-OVIGEROUS FEMALE: as above but lacking brood pouch.

SUB-ADULT MALE: (Fig. 3o). Resembling a non-ovigerous female but bearing penes, separate to base and each 4·5 times as long as broad with a semi-circular tip. Endopod of pleopod 2 with apex slightly extended and an appendix masculina forming beneath the distal cuticle.

ETYMOLOGY: *Bidens,* from the Latin *bi* meaning 'two' + *dens* meaning 'prong'. This refers to the uropodal exopods.

ECOLOGY AND DISTRIBUTION

This species is known only from the upper shore beach rock crevices on Heron Island. It is usually found in crevices occupied by another eubranchiate sphaeromatid, *Dynamenella ptychura* Harrison and Holdich, 1982.

PSEUDOCERCEIS, gen. nov.

GENERIC DIAGNOSIS

Eubranchiate Sphaeromatidae with antennular peduncle article 1 not extended anteriorly as a plate. Anterior margin of cephalosome broadly rounded, not extended anteriorly to cover proximal regions of antennae; median rostral process directed anteroventrally. Rostral process and epistome visible in dorsal view when mouthparts directed anteriorly. Body noticeably convex; coxal plates directed ventrally. Both sexes with pereon and pleon lacking dorsal processes. Pleon with two long suture lines at either side, one reaching the posterolateral angle, and the other the posterior margin, of the pleonal tergite. Pleotelson bearing three prominent, longitudinal ridges. Antennular peduncle article 1 bearing acute distal processes. Maxillipedal palp articles 2 to 4 with pronounced setigerous lobes. Exopod of pleopod 5 bearing two subapical, extended, squamose bosses, one on either side of the ramus, and a smaller simple boss on the internal margin. Uropodal rami lamellar, exopod greater than half length of endopod. Sexual dimorphism slight or not obvious. **Adult male** with penes separate, short, with semicircular tips. Appendix masculina
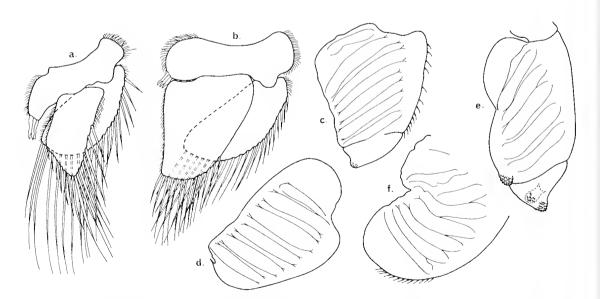
FIG. 4. *Pistorius bidens,* gen. nov., sp. nov. Adult male (a) pleopod 1, (b) pleopod 3, (c) pleopod 4, exopod, (d) pleopod 4, endopod, (e) pleopod 5, exopod, (f) pleopod 5, endopod.

arising from internal margin of endopod of pleopod 2, extending beyond ramal apex to semicircular tips. Apex of pleotelson with a notch which may or may not bear a median tooth. **Ovigerous female** with mouthparts metamorphosed. Brood pouch formed from four pairs of oostegites arising from bases of pereopods 1 to 4. Oostegites increasing in size posteriorly and clearly overlapping at midline. Embryos not held in the marsupium thus formed, but in four pairs of internal pouches. Ventral pockets absent.

ETYMOLOGY: *Pseudocerceis*, from the Greek *pseudo* meaning 'false' + *Cerceis* (feminine).

TYPE SPECIES: *Pseudocerceis furculata*, sp. nov.

ADDITIONAL SPECIES: *Pseudocerceis trilobata* (Baker), comb. nov. for *Cerceis trilobata* Baker, 1908 from Australia. *Pseudocerceis* sp. (see below).

REMARKS

In the form of the appendages, this genus is very close to *Cerceis* Milne-Edwards *sensu stricto*, but differs from it in not having the cephalosome flattened and projecting anteriorly to cover the proximal regions of the antennae, and in being markedly convex, not flattened. All known species of *Pseudocerceis* have three equally prominent projections on the pleotelson. *C. trilobata* Baker lacks the anteriorly extended cephalosome of *Cerceis sensu stricto* (see below) and agrees with the characteristics of *Pseudocerceis* as defined above.

PSEUDOCERCEIS FURCULATA, sp. nov.

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum QM W7959, adult male, 5·52 mm, from intertidal reef flat, Heron Island, SEQ, N.L. Bruce, 15 January 1979.

PARATYPES: QM W7960, subadult male, ovigerous female, data as for holotype. QM W8046, W8049, W8052, W8053, W8058, W8059, W8065, W8067–69, W8072, W8073, 13 adult males, 2 subadult males, 8 ovigerous females, 8 non-ovigerous females, 7 immature specimens, 8 juveniles, intertidal reef flat, Heron Island, SEQ, N.L. Bruce, 5–15 January 1979. QM W8577, adult male, from alga at edge of reef flat, intertidal, Heron Island, SEQ, N.L. Bruce, 6 December 1979. QM W8579, 2 immature specimens, reef crest, boulder zone on north west side, Heron Island, SEQ, N.L. Bruce, 20 November 1979. QM W8578, 2 adult males, ovigerous female, juvenile, edge of reef crest on north east side, Heron Island, SEQ, N.L. Bruce, 6 December 1979. QM W8574, subadult male, reef

edge on north side, Heron Island, SEQ, N.L. Bruce, 4 December 1979. Australian Museum AM P28851, adult male, subadult male, short weed behind reef edge, north side, Wilson Island, Capricorn Group, Queensland (23°18'S, 151°55'E), W.F. Ponder, 4 January 1979. QM W8074, subadult male, on coral rocks in lagoon, depth 1 m, Long Island, Chesterfield Reefs, Coral Sea, N.L. Bruce, 4 May 1979. QM W8075, W8076, subadult male, non-ovigerous female, coral rock in lagoon fringe and reef fringe, depth 1 m, Bennett Island, Chesterfield Reefs (19°55·3'S, 158°23'E), N.L. Bruce, 8 May 1979. QM W8080, non-ovigerous female, coral rock, inner reef, depth 12 m, Bennett Island, N.L. Bruce, 6 May 1979. Heron Island, SEQ, adult male, on dead coral on inner reef flat, intertidal, D.M. Holdich, 11 April 1976. Heron Island, SEQ, adult male, 2 subadult males, non-ovigerous female, 6 immature specimens, 4 juveniles, on *Sargassum* sp., *Laurencia* sp., *Halimeda* sp., *Turbinaria* sp., D.M. Holdich, 13–14 April 1976. Heron Island, southwest reef, subadult male, 2 immature specimens, 4 juveniles, in surf zone at reef edge on algal 'cushions', G. Hartmann, 3 February 1976. Wilson Island, Capricorn Group, ovigerous female, non-ovigerous female, 4 immature specimens, N.L. Bruce, 7 June 1978. Tryon Island, adult male, reef crest, N.L. Bruce, 5 June 1978. Moffat Beach, Caloundra, SEQ, subadult male, N.L. Bruce, 22 June 1978.

DESCRIPTION

ADULT MALE: (Figs 5, 6a–e). Eyes large, lateral. Epistome lambdoid, postero-lateral margins distally dilated, anterior apex acute. Pereon and pleon smooth. Pleotelson granulose with three pronounced, tuberculate ridges; apex with shallow notch obscured by a terminal, subquadrate, extension. Apex of extension emarginate, setose.

APPENDAGES: antennular peduncle article 1 as long as articles 2 and 3 together with two subequal, acute, distal processes; article 2 as long as broad; article 3 three times as long as wide; flagellum with 13 articles, extending to level of pereonite 1. Antenna slender, 13-articled flagellum longer than peduncle, extending to level of pereonite 1. Mouthparts of usual sphaeromatid form, unmodified. Pereopods robust; merus, carpus and propodus bearing inferior pads of short setae. Merus, carpus and propodus of pereopod 1 each with several long, stout, simple spines; pereopods 2 to 7 with more slender spines. Penes each as long as broad. Basis of pleopod 1
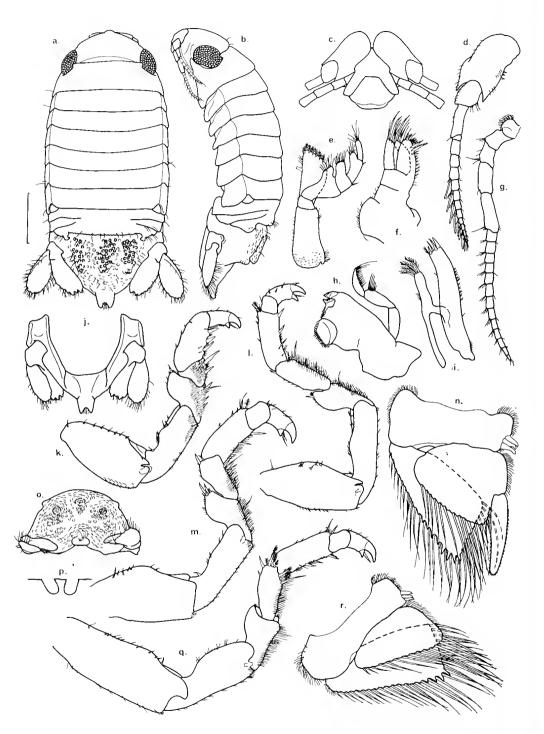
FIG. 5. *Pseudocerceis furculata,* gen. nov., sp. nov. Adult male (a) dorsal, (b) lateral, (c) epistome, labrum and penduncles of antennae, (d) antennule, (e) maxilliped, (f) maxilla, (g) antenna, (h) left mandible, (i) maxillule, (j) pleotelson, ventral, (k–m) pereopods 1, 2 and 4 respectively, (n) pleopod 2, (o) pleotelson, posterior, (p) penes, (q) pereopod 7, (r) pleopod 1. Scale line represents 1 mm.

with three internal coupling hooks; endopod short, subtriangular; exopod truncate with five external teeth. Pleopod 2 with endopod subtriangular, just shorter than truncate exopod; exopod bearing ten external teeth. Appendix masculina subequal in length to endopod, tapering slightly distally with apex rounded. Pleopod 3 with endopod subtriangular, subequal in length to subelliptical exopod; exopod without an articulation. Exopod of pleopod 4 with a proximal, external, triangular, toothed boss. Exopod of pleopod 5 with a complete, subterminal articulation. Uropodal rami subequal, subelliptical, not reaching level of pleotelsonic apex; distal margin of endopod irregularly dentate; distal margin of exopod weakly crenulate.

COLOUR OF SPECIMENS IN ALCOHOL: cream with dorsal surface of body covered with small brown chromatophores. Chromatophores also present on antennular peduncles, bases of pleopods, and uropods, but are absent from the pereopods. Some male specimens with chromatophores on ventral pereon, and pleotelson bearing dense chromatophores.

OVIGEROUS FEMALE, 4·6 mm: (Fig. 6f, i, k–n). Cephalosome short, strongly convex. Pleotelson with three low, longitudinal ridges, the central being the most prominent. Apex of pleotelson with a ventral notch overhung by a short, broad tooth. Antennae as in adult male. Mouthparts metamorphosed. Mandible fused proximally with cephalosome, apex as a simple lobe; palp unmodified, fully formed. Maxillule with two simple lobes lacking long setae. Maxilla with three simple lobes lacking long setae. Maxilliped with palp reduced, extending only to apex of endite, lobes on articles 2 to 4 lacking long setae; endite proximally expanded as one internal lobe with fine marginal setae, a small external lobe with long plumose setae and a longer external lobe with fine marginal setae. Pereopods lacking dense inferior pads of setae. Pleopods as in adult male (but lacking appendix masculina). Uropods with rami subequal in length, extending to level of pleotelsonic tip with apices rounded, dentate.

SUBADULT MALE: (Fig. 6g, h, j). In dorsal view, resembling ovigerous female but cephalosome less convex and pleotelsonic apex with blunt median tooth more pronounced. This tooth shows variation in size between individuals and in larger forms may be weakly bifid. Penes as low, separate papillae. Tissue of appendix masculina can be seen differentiating beneath cuticle of endopod of pleopod 2.

NON-OVIGEROUS FEMALE: As subadult male (excepting primary sexual characteristics) but median tooth of pleotelsonic apex short.

ETYMOLOGY: *Furculata,* Latin meaning 'with a small fork'.

ECOLOGY AND DISTRIBUTION
Apart from one specimen recorded from Caloundra, a mainland site, this species has only been recorded from islands off the Queensland coast and in the Coral Sea. It has mainly been found associated with intertidal coral or algae on reef flats.

REMARKS
In dorsal view the male of this species bears some resemblance to illustrations of *Holotelson tuberculatus* Richardson. Examination of specimens of *H. tuberculatus* in collections of the British Museum shows this species to be generically distinct. The genus *Holotelson* Richardson is closely related to the genus *Dynamenopsis* Baker and *H. tuberculatus* has a thick, heavily calcified cuticle, and the incisor process of the mandible is smoothly rounded. The pleopods of *H. tuberculatus* lack marginal teeth and are not of cerceid form. The female of *H. tuberculatus* was described by Vanhöffen (1914: 56–59) as his 'new species', *Cassidias trituberculata.*

PSEUDOCERCEIS sp.

MATERIAL EXAMINED
Lodestone Reef (east of Townsville), Queensland, adult male, ovigerous female, non-ovigerous female, 3 immature specimens, 5 juveniles, from dead coral and algae in reef flat pools, intertidal, I. Price, 1976.

DESCRIPTION
ADULT MALE: (Fig. 6o, p, r, s). This specimen is anteriorly badly damaged. Pleotelson granulose bearing three pronounced tuberculate ridges; apex with a shallow notch obscured by an extended, terminal process. Process twice as long as broad with short, dorsal setae, lateral margins parallel, apex upturned, deeply emarginate, setose. Pleopod 2 with exopod bearing six external teeth; appendix masculina subequal in length to endopod, internal margin bearing, a long, shallow indentation in distal half, apex broadly rounded. Uropod with endopod subelliptical, not extending as far as pleotelsonic apex, external margin serrate, distal margin irregularly dentate; dorsal surface with
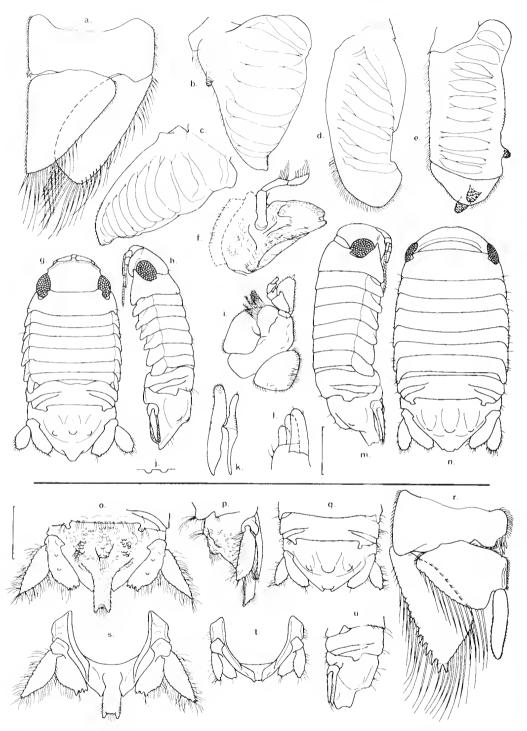
FIG. 6. *Pseudocerceis furculata,* gen. nov., sp. nov. Adult male (a) pleopod 3, (b) pleopod 4, exopod, (c) pleopod 4, endopod, (d) pleopod 5, endopod, (e) pleopod 5, exopod. Ovigerous female (f) right mandible, (i) maxilliped, (k) maxillule, (l) maxilla, (m) lateral, (n) dorsal. Subadult male (g) dorsal, (h) lateral, (j) penes. *Pseudocerceis* sp. Adult male (o) pleotelson, (p) pleotelson, lateral, (r) pleopod 2, (s) pleotelson, ventral. Ovigerous female (q) pleon and pleotelson, dorsal, (t) pleotelson, ventral, (u) pleon and pleotelson, lateral. Scale line represents 1 mm.

one proximal and one median tubercle; exopod longer than endopod, narrowly lanceolate; margins of both rami bearing long setae.

OVIGEROUS FEMALE: (Fig. 6q, t, u). As ovigerous female of *P. furculata* sp. nov., but pleotelsonic notch more pronounced with median tooth shorter, and apex of uropodal exopod slightly acute.

ECOLOGY AND DISTRIBUTION
Known only from dead coral and algae on Lodestone Reef, east of Townsville.

REMARKS
This species is clearly separated from *P. furculata,* sp. nov. by its longer pleotelsonic process and lanceolate uropodal exopod. Unfortunately the only adult male seen was extensively damaged and the authors do not consider it wise to fix this male as the type specimen by describing it as a new species.

CERCEIS Milne-Edwards, 1840
Cerceis Milne-Edwards, 1840: 220, 221.
Paradynamene Richardson, 1905: 305.
New synonym.
Circeis Baker, 1908: 153. — Nierstrasz, 1931: 215 (unjustified emendation).

GENERIC DIAGNOSIS
Eubranchiate Sphaeromatidae with antennular peduncle article 1 not extended anteriorly as a plate. Anterior margin of cephalosome narrowly rounded, extended anteriorly to cover proximal regions of antennae. Median rostral process directed posteroventrally; rostral process and epistome never visible in dorsal view. Body markedly flattened, not strongly domed; coxal plates closely applied forming a continuous lateral margin. Both sexes with pereon and pleon lacking dorsal processes. Pleon with two long suture lines at each side, one reaching the posterolateral angle, and the other the lateral margin, of the pleonal tergite. Antennular peduncle article 1 bearing acute distal processes. Maxillipedal palp articles 2 to 4 with pronounced setigerous lobes. Exopod 5 bearing two subapical, extended, squamose bosses, one either side of the ramus, and a smaller boss — simple or bifid — on the internal margin. Uropodal rami lamellar, exopod greater than half length of endopod. Sexual dirmophism not pronounced. **Adult male** with penes separate, short, with semicircular tips. Appendix masculina arising from internal margin of endopod of pleopod 2, extending beyond ramal apex to a

semicircular tip. Apex of pleotelson with a notch which may or may not bear a median tooth. **Ovigerous female** with mouthparts metamorphosed. Brood pouch formed from four pairs of oostegites arising from bases of pereopods 1 to 4. Oostegites increasing in size posteriorly and overlapping well in the midline. Brood not housed in the marsupium thus formed (cf. Hansen, 1905: 108) but in four pairs of internal pouches. Ventral pockets absent.

TYPE SPECIES: *Cerceis tridentata* Milne-Edwards, 1840 (from Australia)

ADDITIONAL SPECIES: *Cerceis bidentata* Milne-Edwards, 1840 (from Australia) *Cerceis acuticaudata* (Haswell, 1882) (from Australia) *Cerceis picta* Nierstrasz, 1931 (from Philippines) *Cerceis bicarinata* Barnard, 1936 (from the Andaman Islands) *Cerceis granulata* Pillai, 1954 (from India) *Cerceis orientalis* (Dana, 1853) (immature specimens) (from Singapore) *Cerceis aspericaudata* Miers, 1884, comb. nov. (from Australia) *Cerceis pravipalma,* sp. nov. *Cerceis pustulosa,* sp. nov.

REMARKS
Other species currently in the genus *Cerceis* are not obviously members of this group. *Cerceis trilobata* Baker, 1908 has been transferred to the genus *Pseudocerceis* above. *Cerceis carinata* Glynn, 1970, from Venezuela, differs in the form of the pleonal sutures, the penes and the appendix masculina; article 1 of the antennular peduncle lacks the acute processes; and the cephalosome is not extended anteriorly to cover the antennae. In the three remaining species, all from Australia, *(Cerceis trispinosa* Haswell, 1882; *Cerceis obtusa* Baker, 1908; and *Cerceis ovata* Baker, 1926) the cephalosome does not extend anteriorly to cover the antennae and the pleon is much shorter than in

specimens of *Cerceis sensu stricto*. The correct generic placement of these species is at present unknown.

CERCEIS PUSTULOSA, sp. nov.

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum QM W7964, adult male 11·0 mm, on sub-littoral algae and lower shore algae, Alma Bay, Magnetic Island, Townsville, Queensland (19°10'S, 146°50'E), D.M. Holdich, 9 July 1976.

PARATYPES: QM W7965, subadult male, 6 non-ovigerous females, 3 immature specimens, 3 juveniles, same data as holotype. Picnic Bay, Magnetic Island, in coral rubble, intertidal, juvenile, D.M. Holdich, 17 March 1976. Horseshoe Bay, Magnetic Island, from floating *Sargassum* sp., 3 immature specimens, D.M. Holdich, 24 April 1976.

DESCRIPTION

ADULT MALE: (Fig. 7a–j, m). *Cerceis* with eyes large, lateral. Epistome lambdoid with sinuous lateral margins and an acute apex. Each pereonal tergite with posterior margin bearing a lateral row of short setae. Dorsal surface of pereonite 7 laterally granulose. Pleon and pleotelson covered with short setae. Pleon posteriorly granulose. Pleotelson with a low, anteromedian, finely granulose boss bearing a prominent posterior tubercle, and a long tuberculate protuberance each side of the median boss. Apex of pleotelson with a deep notch, filled by a large, blunt, triangular, granulose, overhanging process, extending beyond level of notch opening; at each side of proximal region of process is a small circular foramen.

APPENDAGES: antennular peduncle article 1 longer than articles 2 and 3 together with two acute distal processes enclosing article 2, the inferior process being longer than the superior; article 2 short with a short, curved, posterior tooth; article 3 slender, curved; 17-articled flagellum extending to level of pereonite 1. Antenna slender, flagellum extending to level of pereonite 3. Mouthparts of usual sphaeromatid form, unmodified. Pereopods robust; merus, carpus and propodus bearing inferior pads of short setae. Merus, carpus and propodus of pereopod 1 with an inferior row of long simple spines. Penes each three times as long as broad. Basis of pleopod 1 with three internal coupling hooks; endopod short, subtriangular; exopod truncate with 10 pronounced external teeth. Pleopod 2 with

endopod subtriangular; exopod truncate with 17 pronounced external teeth. Appendix masculina just longer than endopod; broad proximally, tapering to mid point; distal half with lateral margins subparallel; apex narrowly rounded, curved slightly towards animal's midline. Exopod of pleopod 3 with a complete subterminal articulation. Exopod of pleopod 4 with a triangular, proximal, external toothed boss. Exopod of pleopod 5 with one small, internal, marginal, toothed boss and two larger subterminal bosses. Endopod of uropod superiorly granulose and setose in external half; extending beyond pleotelsonic apex with distal margin irregular, anterodistal and posterodistal angles bearing posteriorly directed processes; exopod longer than endopod, broadly lanceolate with an acute apex; ventral surface of endopod convex, granulose.

COLOUR OF SPECIMENS IN ALCOHOL: cream with a single transverse row of faint chromatophores along the posterior margin of the tergite of pereonite 7.

SUBADULT MALE: (Fig. 7k, n, o, p, r). *Cerceis* with dorsal surface of body smooth. Each pereonal tergite with posterior margin bearing a row of short setae. Pleotelson dorsally setose with a low anteromedian boss and a low protuberance either side of this. Pleotelsonic apex with a broad notch filled by a broad median, triangular tooth extending beyond notch opening. Penes each twice as long as broad. Endopod of pleopod 2 with appendix masculina forming beneath cuticle, not externally visible. Endopod of uropod dorsally setose with distal margin irregular, anterodistal angles and posterodistal angles bearing posteriorly directed processes; exopod lanceolate with an acute tip and a serrate internodistal margin.

NON-OVIGEROUS FEMALE: (Fig. 7l, q). As subadult male (excepting primary sexual characters) but tooth in pleotelsonic notch short, extending only to level of notch opening.

ETYMOLOGY: *Pustulosa*, Latin meaning 'full of pimples'.

ECOLOGY AND DISTRIBUTION

Known only from Magnetic Island, Australia where it was collected from littoral and sub-littoral algae and coral rubble.

REMARKS

This species closely resembles *Cerceis granulata* from India but differs in the form of the dorsal pleotelsonic tuberculation; the shape of the uropodal exopod; the shape of the appendix masculina; and in having a relatively longer pleon.
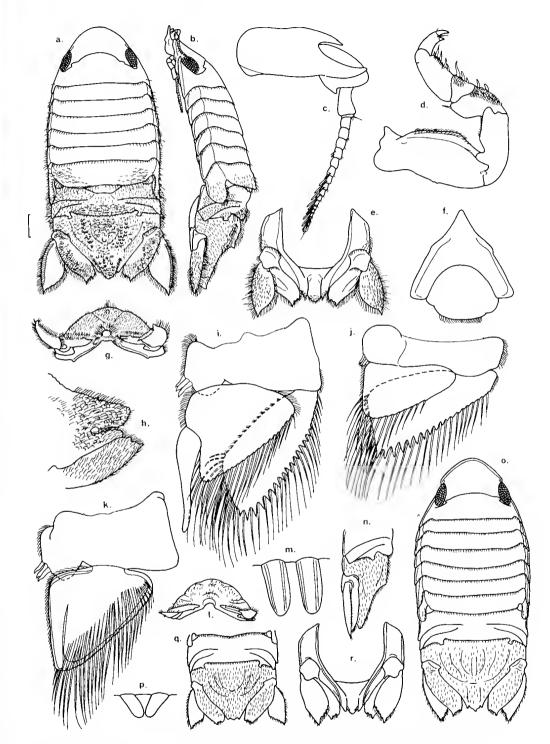
FIG. 7. *Cerceis pustulosa*, sp. nov. Adult male (a) dorsal, (b) lateral, (c) antennule, (d) pereopod 1, (e) pleotelson, ventral, (f) epistome and labrum, (g) pleotelson, posterior, (h) pleotelsonic apex, dorsolateral, (i) pleopod 2, (j) pleopod 1, (m) penes. Subadult male (k) pleopod 2 (exopod omitted), (n) pleotelson, lateral, (o) dorsal, (p) penes, (r) pleotelson, ventral. Non-ovigerous female (l) posterior, (q) pleon and pleotelson. Scale line represents 1 mm.

CERCEIS PRAVIPALMA, sp. nov.

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum QM W7966, male, 6·9 mm, on *Sargassum* sp. on muddy shore with dead coral, mid-shore, Yule Point, Cairns, Queensland (16°51'S, 145°43'E), D.M. Holdich, 29 May 1976.

PARATYPES: QM W7967, subadult male, immature specimen, juvenile, data as for holotype. Australian Museum AM P28820 (+ microslide of pleopods), semi-moulted adult male, vicinity of Thursday Island, Torres Strait, Queensland, P.C. Young (CSIRO Fisheries and Oceanography), April 1979.

DESCRIPTION

ADULT MALE: (Figs 8a–i, k, l, 9a–f). *Cerceis* with eyes large, lateral. Epistome lambdoid with sinuous lateral margins and an acute apex. Each pereonal tergite with posterior margin bearing a lateral row of short setae. Lateral margins of body bearing long setae. Pleon and pleotelson covered with short setae. Pleon with posterior sutures restricted to posterior third; posterior margin with a row of small tubercles. Pleotelson granulose with a low median protuberance either side of midline and a smaller anteromedian boss. Apex of pleotelson with a deep, quadrate notch and a large triangular, blunt, median process not reaching level of notch opening.

APPENDAGES: antennular peduncle article 1 longer than articles 2 and 3 together with two acute distal processes enclosing article 2, the inferior process being longer than the superior; flagellum extending to level of pereonite 1. Antenna slender, flagellum extending to level of pereonite 3. Mouthparts of usual sphaeromatid form, unmodified. Pereopods robust; merus, carpus and propodus bearing inferior pads of short setae. Merus, carpus and propodus of pereopod 1 with an inferior row of long, stout, simple spines. These articles of pereopods 2 to 7 with fewer, less stout spines. Penes each four times as long as broad. Basis of pleopod 1 with three internal coupling hooks; endopod short, subtriangular; exopod long, truncate with four pronounced external distal teeth. Pleopod 2 with endopod broader than long; exopod truncate with 15 pronounced external teeth. Appendix masculina 1½ times length of endopod, narrow, tapering slightly to narrowly rounded apex with an external, subterminal indentation. Pleopod 3 with endopod subtriangular, elongate, subequal in length to subelliptical exopod; exopod with a complete, subterminal articulation. Exopod of

pleopod 4 with a triangular, proximal, external toothed boss. Exopod of pleopod 5 with a complete subterminal articulation and one small internal, marginal, toothed boss, and two larger subterminal bosses. Endopod of uropod superiorly granulose and setose, extending beyond pleotelsonic apex with distal margin irregular, anterodistal and posterodistal angles bearing posteriorly directed processes; exopod just longer than endopod with apex acute, lateral margins bearing long setae, dorsal surface concave, and internal margin distally notched and subapically crenulate.

COLOUR OF SPECIMEN IN ALCOHOL: cream, lacking chromatophores.

SUBADULT MALE: (Fig. 8j, m–o). *Cerceis* with dorsal surface of body smooth. Each pereonal tergite with posterior margin bearing a lateral row of short setae. Pleon with posterior sutures restricted to posterior third. Pleotelson dorsally setose with a low median protuberance either side of midline and a smaller anteromedian boss. Pleotelsonic apex with a shallow notch with a short, median, overhanging process. Penes each twice as long as broad. Endopod of pleopod 2 with appendix masculina forming beneath cuticle, not externally visible. Endopod of uropod dorsally setose, smooth, with posterodistal angle extended as an acute process; exopod broadly lanceolate, internal margin not notched or subapically crenulate.

ETYMOLOGY: *Pravipalma*, from the Latin *pravus* meaning 'deformed', + *palma* meaning 'an oar blade'. This refers to the uropodal exopod.

ECOLOGY AND DISTRIBUTION

Known only from intertidal seaweed near Cairns, and from the Torres Straits in Northern Queensland.

REMARKS

This species does not clearly resemble any of the known species. It can be distinguished from *C. pustulosa*, sp. nov. by its indented uropodal exopods; its shorter median, apical, pleotelsonic process; the form of the appendix masculina; and by its relatively longer pleon.

CERCEIS ASPERICAUDATA Miers, 1884 comb. nov.

Cerceis bidentata Milne-Edwards, var. *aspericaudata* Miers, 1884: 306, 307, 666, pl. 33.
Paradynamene benjamensis Richardson, 1905: 305–7. Nierstrasz, 1931: 212. Menzies and Frakenberg, 1966: 9. Schultz, 1969: 121.
New Synonym.
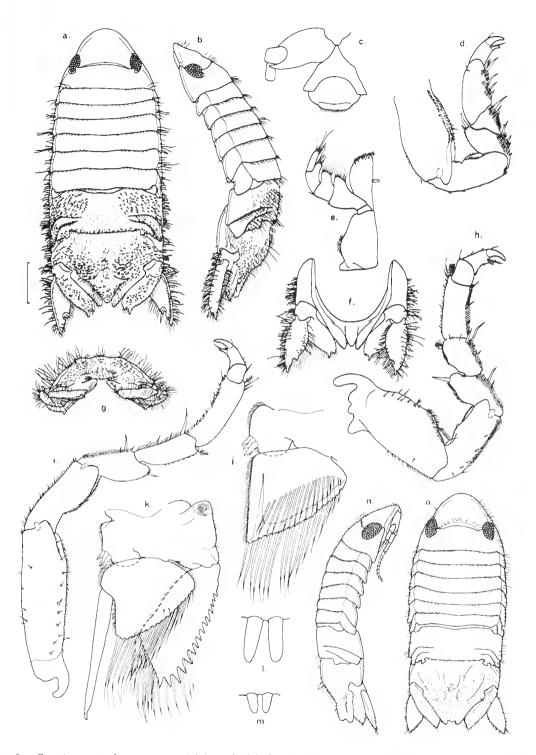
FIG. 8. *Cerceis pravipalma,* sp. nov. Adult male (a) dorsal, (b) lateral, (c) epistome, labrum and antennular peduncle, (d) pereopod 1, (e) maxilliped, (f) pleotelson, ventral, (g) pleotelson, posterior, (h) pereopod 5, (i) pereopod 7, (k) pleopod 2, (l) penes. Subadult male (j) pleopod 2 (exopod omitted), (m) penes, (n) lateral, (o) dorsal. Scale line represents 1 mm.

Cerceis   tridentata   Milne-Edwards,   var.
    intermedia Baker, 1926: 270, 279, pl. 50.
    Nierstrasz, 1931: 216.
Circeis tridentata var. *aspericaudata:* Nierstrasz,
    1931: 216.

MATERIAL EXAMINED

HOLOTYPE: British Museum (Natural History)
BM (NH) 1882. 7, adult male, 12·4 mm, depth
12·8 m, Prince of Wales Channel, Torres Strait,
Queensland, H.M.S. Alert.

OTHER MATERIAL: Queensland Museum QM
W7970, 5 non-ovigerous females, 2 juveniles, on
Sargassum sp., sub-littoral fringe, Kurrimine,
Queensland (17°54'S, 146°05'E), D.M. Holdich,
27 May 1976. Alma Bay, Magnetic Island,
Queensland, from algae and wood on old pier pile,
intertidal, non-ovigerous female, D.M. Holdich,
26 April 1976. Bay of Rest, Exmouth Gulf,
Western Australia, on *Sargassum* sp., intertidal,
subadult male, 2 immature specimens, juvenile,
N.L. Bruce, 12 June 1980. Bundegi Reef,
Exmouth Gulf, on *Sargassum* sp., intertidal, 3
subadult males, 3 non-ovigerous females, imma-
ture specimen, 3 juveniles, N.L. Bruce, 14 July
1978.

DESCRIPTION

ADULT MALE: (Fig. 9g, i–l, n–p). *Cerceis* with
eyes large, lateral. Epistome lambdoid, smoothly
convex with arcuate lateral margins. Each
pereonal tergite with posterior margin bearing a
lateral row of short setae. Posterior margins of
pereonite 7 and pleon, and pleonal sutures,
bearing rows of small tubercles. Pleotelson
granulose with a short, low, anterior, median boss
with a similar but longer boss at each side. Apex
of pleotelson narrow, with a deep, acute, lambdoid
notch. Anterior to notch is a broad, long, acute
tooth with a small circular foramen at each side of
the base.

APPENDAGES: antennule with peduncle
article 1 longer than articles 2 and 3 together with
two acute distal processes enclosing article 2, the
inferior process being longer than the superior;
12-articled flagellum extending to level of
pereonite 1. Antenna slender, flagellum subequal
in length to peduncle, extending to level of
pereonite 3. Appendix masculina extending well
beyond apex of endopod of pleopod 2; broad
proximally, tapering distally, to a narrowly
rounded tip, slender in distal half and curved away
from ramus. Endopod of uropod with anterodistal
angle arcuate, posterodistal angle extended as an

acute process extending well beyond level of
pleotelsonic apex; exopod longer than endopod,
external   margin granulose, arcuate, internal
margin convex, tapering to a narrow acute tip.

COLOUR OF SPECIMEN IN ALCOHOL: cream,
lacking chromatophores.

SUBADULT MALE: (Fig 9h q, r). *Cerceis* with
eyes large, lateral. Epistome lambdoid, smoothly
convex with arcuate lateral margins. Pereon and
pleon smooth. Pleotelson with a low boss either
side of midline; each boss bearing a low irregular
tubercle. Apex of pleotelson with a deep notch
with a short, blunt, median tooth. Penes widely
separate, each as long as broad. Appendix
masculina forming within cuticle of endopod of
pleopod 2.

NON-OVIGEROUS FEMALE: (Fig. 9m). As
subadult male but pleotelsonic notch without a
median tooth.

ECOLOGY AND DISTRIBUTION

In Queensland known from Kurrimine and
Magnetic Island from intertidal algae. Also
recorded from the Torres Straits and on intertidal
algae in Western Australia.

REMARKS

Miers' (1884) variety does not fit closely the
description of *C.   bidentata* given by Milne-
Edwards and its elevation to full specific status is
considered necessary.

Nierstrasz (1931) reported this species as *C.
tridentata* var. *aspericaudata*, presumably
because Hansen (1905: 127) stated that *C
bidentata* was the female of *C. tridentata* or a
closely related species. Nierstrasz did not mention
C. bidentata and was presumably treating it as a
junior synonym of *C. tridentata*. *C. bidentata* is
retained here as it is known only from
Milne-Edwards' description and its conspecificity
with *C. tridentata* is not certain.

Comparison of the adult male type specimen of
Paradynamene benjamensis Richardson with
Miers' holotype of *C. aspericaudata* shows that
the two specimens are taxonomically indistin-
guishable and *P. benjamensis* should be
considered a junior synonym.

Australian specimens agreeing with Baker's
description of *C. tridentata* var. *intermedia* were
compared with a subadult male and a non-
ovigerous female (type specimens) of *P.
benjamensis* and were found to be identical. *C.
tridentata* var. *intermedia* is therefore founded on
immature specimens of *C. aspericaudata*.
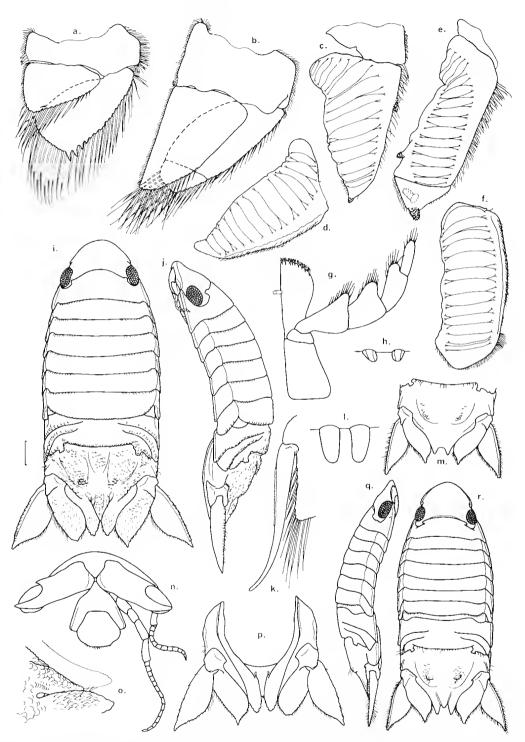
FIG. 9. *Cerceis pravipalma,* sp. nov. Adult male (a) pleopod 1, (b) pleopod 3, (c) pleopod 4, exopod, (d) pleopod 4, endopod, (e) pleopod 5, exopod, (f) pleopod 5, endopod. *Cerceis aspericaudata* Miers, comb. nov. Adult male (holotype), (g) maxilliped, (i) dorsal, (j) lateral, (k) appendix masculina, (l) penes, (n) cephalosome, ventral, (o) pleotelsonic apex, dorsolateral, (p) pleotelson, ventral. Subadult male (h) penes, (q) lateral, (r) dorsal. Non-ovigerous female (m) pleotelson. Scale represent 1 mm.

Paradynamene benjamensis was described by Richardson (1905) in her monograph on the isopods of North America. The specimens came from a bottle marked 'Gulf Weed' in the Museum of Comparative Zoology at Harvard University. The collector, date of collection and collection locality were unknown. Richardson presumably assumed 'Gulf' to indicate the Gulf of Mexico and the fact that these specimens were in an American museum probably reinforced the assumption that they were from North American waters. Menzies and Frankenberg (1966) stated that *P. benjamensis* might occur off the Georgian coast, but referred only to Richardson's original publication. Schultz (1969) apparently put these two 'records' together when he said for *P. benjamensis,* "Range: Atlantic coast and in Gulf Stream. This species was found in floating algae in the Gulf Stream". In fact, no record of *P. benjamensis* has ever been confirmed from North America. As this species is identical to *C. aspericaudata,* a species known only from Australia, it seems most likely that the type specimens of *P. benjamensis* were collected from weed in an unknown gulf in Australia, and it is interesting to note that specimens of *C. tridentata* var. *intermedia* have been collected from floating *Sargassum* sp. in the Gulf of Carpentaria (*fide* Baker, 1926: 270) and from this weed in Queensland and Western Australia. There is no reason to believe that *C. aspericaudata* occurs anywhere other than in Australia.

PARACERCEIS Hansen, 1905

Paracerceis Hansen, 1905: 77, 83, 87, 90, 91, 108, 125–27.
Paracirceis Nierstrasz, 1931: 215 (unjustified emendation).
Sergiella Pires, 1980: 212–218. Pires, 1981: 219, 220.

GENERIC DIAGNOSIS

Eubranchiate Sphaeromatidae with antennular peduncle article 1 not extended anteriorly as a plate. Both sexes with pereon and pleon lacking dorsal processes. Pleon with posterior margin bearing two curved, parallel sutures at each site. Exopod of pleopod 5 with three equidistant, extended, squamose bosses — one apical and two internal. Sexual dimorphism pronounced. **Adult male** with penes separate to base, broad, with semicircular tips. Appendix masculina arising in distal half of endopod of pleopod 2, extending beyond ramal apex to a semi-circular tip. Pleotelsonic apex extended with a wide median notch bearing one or more acute teeth. Uropodal endopod short, reaching, at most, half way to pleotelsonic apex; exopod long, narrow, often cylindrical, extending beyond pleotelsonic apex. Maxillipedal palp articles 2 to 4 bearing pronounced setigerous lobes. **Ovigerous female** with mouthparts strongly metamorphosed. Brood pouch formed from four pairs of oostegites arising from percopods 1 to 4 and overlapping in the midline. Oostegites increasing in size posteriorly. Brood not housed in narsupium thus formed but in internal pouches. Ventral pockets absent. Pleotelsonic apex slightly extended, lacking a toothed notch but bearing a semicircular ventral channel, visible in posterior view. Uropodal rami lamellar, subequal in length, not reaching apex of pleotelson. Pleotelsonic tuberculation less pronounced than in adult male.

TYPE SPECIES: *Paracerceis caudata* (Say, 1818) (from south eastern North America).

ADDITIONAL SPECIES: *Paracerceis cordata* (Richardson, 1899) (from west coast of N. America).
P. gilliana (Richardson, 1899) (from California).
P. sculpta (Holmes, 1904) (from California, Mexico, Brazil, Hawaii and Australia).
P. beddardi (Stebbing, 1905) (from Sri Lanka).
P. edithae (Boone, 1930) (from Puerto Rico and Haiti).
P. angulata (Richardson, 1901) (from Florida — adult male unknown).
P. nuttingi (Boone, 1921) (from Barbados — adult male unknown).
P. tomentosa (Schultz & McCloskey, 1967) (from North Carolina — adult male unknown).

PARACERCEIS SCULPTA (Holmes, 1904)

Dynamene sculpta Holmes, 1904: 300–302, pl. 34.
Cilicaea sculpta Richardson, 1905: 318, 319. Stebbing, 1905: 35.

Paracerceis sculpta Richardson, 1905: IX.
  Menzies, 1962: 340, 341, fig. 2. Miller, 1968: 9,
  14. Pires, 1981: 219, 220.
Sergiella angra Pires, 1980: 212–218. Pires, 1981:
  219, 220.

MATERIAL EXAMINED
  Queensland Museum QM W7968, adult male,
non-ovigerous female, from side of pontoon near
Hayle's Wharf, Ross River Creek, Townsville,
Queensland (19°16'S, 146°49'E), P. Otteson,
October 1975.

DESCRIPTION
  ADULT MALE, 7·82 mm: (Fig. 10a–p, s). Dorsal
surface of cephalosome and pereon smooth. Eyes
large, lateral. Epistome with a short apex between
two pronounced lateral bulges. Pereonite 7 with
posterior margin of tergite granulose. Pleon
granulose with a low, bifid, central tubercle and
one simple tubercle on each side. Pleotelson with
main dome granulose, bearing three pronounced
longitudinal ridges, the central being dorsally
concave. Posterior to main dome, pleotelson
bearing an intricate, symmetrical arrangement of
short setae surrounding a prominent median
conical tubercle. Lateral margins of pleotelson
straight, apex extended with a broad deep median
notch. Notch with a central anterior tooth and a
larger curved anterolateral tooth at each side.
Posterior margin of pleotelson, between notch and
lateral margins, slightly indented.
  APPENDAGES: antennular peduncle article 1
longer than 2 and 3 together, not bearing long,
acute, distal extensions; article 2 broader than
long, article 3 slender; 11-articled flagellum
extending to level of pereonite 1. Antenna slender,
13-articled flagellum extending to level of
pereonite 1. Mouthparts of usual sphaeromatid
form, unmodified; maxillipedal palp articles 2 to 4
with pronounced setigerous lobes. Pereopods
moderately robust; merus, carpus and propodus
bearing inferior pads of short setae and spines of
various lengths. Pereopod 1 more robust than
other pereopods; merus, carpus and propodus
bearing long, stout, inferior spines. Penes short,
each 1·5 times as long as broad. Basis of pleopod 1
with three internal coupling hooks; endopod
subtriangular, half size of exopod; exopod broad,
truncate, extending beyond endopod with two
apical teeth and an external, submarginal row of
setae. Pleopod 2 with exopod as in pleopod 1 but
with ten external teeth; endopod subtriangular;
appendix masculina broad with lateral margins
subparallel, extending well beyond endopodal

apex. Exopod of pleopod 3 with a complete
subterminal articulation. Exopod of pleopod 4
with a proximal external toothed boss. Exopod of
pleopod 5 with a subterminal, external, partial
articulation. Uropod with endopod reduced,
bearing a median dorsal tubercle, apex acute;
exopod smooth, greatly extended, curved,
subcylindrical, tapering to a narrowly rounded
apex.
  COLOUR OF SPECIMEN IN ALCOHOL: red-
brown, lacking obvious chromatophores.
  NON-OVIGEROUS FEMALE, 5·34 mm: (Fig. 10q,
r, t). *Paracerceis* with dorsal surface of body
smooth. Pleotelson with three low, smooth
longitudinal ridges; apex slightly extended with a
simple ventral groove. Uropodal rami subequal,
not reaching pleotelsonic apex; endopod truncate;
exopod rounded.

DISTRIBUTION
  This species has previously been recorded from
California, Brazil, Mexico and Hawaii. It has
presumably been carried to Townsville (an
international harbour) by trans-Pacific shipping.

REMARKS
  The illustrated male specimen bears a number
of spirorbid polychaete tubes on the pleotelson.
The growth of epibionts, especially on the
pleotelson, is not uncommon in certain sphaer-
omatids, e.g. adult male specimens of *Dynamene*.

HASWELLIA Miers, 1884
Calyptura Haswell, 1881: 476 (preoccupied
  name).
Haswellia Miers, 1884: 311.

GENERIC DIAGNOSIS
  Eubranchiate Sphaeromatidae with antennular
peduncle article 1 not extended anteriorly as a
plate. Pleon with two long suture lines at either
side, one reaching the posterolateral angle, and the
other the lateral margin, of the pleonal tergite.
Exopod of pleopod 5 bearing two subapical,
extended, toothed bosses, one on either side of the
ramus, and a small prominent internal boss.
Sexual dimorphism pronounced. **Adult male** with
penes separate, short, each with a semicircular tip.
Appendix masculina arising in distal half of
endopod of pleopod 2, extending beyond ramal
apex to a semicircular tip. Tergum of pereonite 7
extended posteriorly as a broad process, reaching
beyond pleotelsonic apex. Apex of pleotelson with
a deep notch bearing a median tooth. Uropodal
rami various, exopod greater than half length of
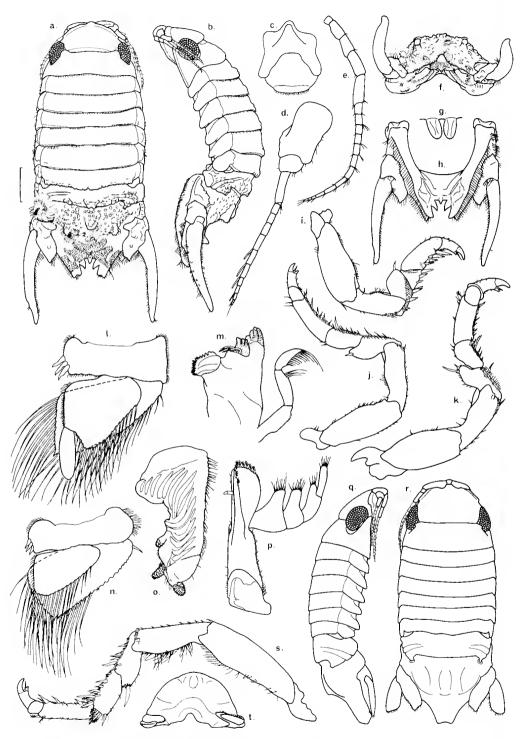
FIG. 10. *Paracerceis sculpta* (Holmes). Adult male (a) dorsal, (b) lateral, (c) epistome and labrum, (d) antennule, (e) antenna, (f) pleotelson, posterior, (g) penes, (h) pleotelson, ventral, (i–k) pereopods 1, 2 and 4 respectively, (l) pleopod 2, (m) left mandible, (n) pleopod 1, (o) pleopod 5, exopod, (p) maxilliped, (s) pereopod 7. Non-ovigerous female (q) lateral, (r) dorsal, (t) posterior. Scale line represents 1 mm.

endopod, extending beyond pleotelsonic apex. Maxillipedal palp articles 2 to 4 bearing setigerous lobes. **Ovigerous female** with mouthparts strongly metamorphosed. Brood pouch formed from four pairs of oostegites arising from bases of pereopods 1 to 4. Oostegites increasing in size posteriorly and overlapping well in midline. Brood not housed in marsupium thus formed but in four pairs of internal pouches. Ventral pockets absent. Tergum of pereonite 7 not extended posteriorly as a process. Pleotelson bearing a median protuberance; apex at most weakly tridentate with a ventral channel. Rami of uropods lamellar, subequal, reaching level of pleotelsonic apex.

TYPE SPECIES: *Haswellia carnea* (Haswell, 1881) (from Australia).

ADDITIONAL SPECIES: *Haswellia emarginata* (Haswell, 1882) (from Australia).
H. cilicoides Baker, 1908 (from Australia).
H. juxtacarnea Baker, 1926 (from Australia).
H. intermedia Baker, 1926 (from Australia).
H. glauerti Baker, 1929 (from Australia).
H. anomala Haswell, 1881 (from Australia — adult male unknown).

REMARKS

Haswell (1881: 473, Pl. 16) described the subadult male of a species of *Haswellia* as *Sphaeroma* (?) *anomala*. Baker (1926: 273) said this species bore some resemblance to the females of *Haswellia emarginata* and Naylor (1966: 192, 194) and Seed (1973: 211) synonymised the two species as *Haswellia anomala*. Comparison by the present authors of a subadult male specimen of *H. emarginata* (together with Baker's illustration of a subadult male — 1908: pl. 10, fig. 4), with specimens of *Sphaeroma anomala* in the British Museum (Natural History) (reg. nos 95. 11. 4. 40–41) (together with Haswell's (1881: pl. 16, fig. 4) and Baker's (1926: pl. 48, figs 8, 9) illustrations of *S. anomala*) shows some differences. The subadult males of *H. emarginata* differ from specimens of *H. anomala* in having the extension of pereonite 7 bilobed, not simple, and relatively shorter. The shape of the uropodal endopod also differs in the two species. While doubt exists that *H. emarginata* and *H. anomala* are conspecific, it seems wise to keep the two names separate. *H. anomala* was originally described from Port Jackson at the same time as *H. carnea* (also from Port Jackson) and it is possible that *H. anomala* is the subadult male of that species. Females and immature specimens of *H. carnea* have never been described.

HASWELLIA CARNEA (Haswell 1881)
Calyptura carnea Haswell, 1881: 476, pl. 17, fig. 4.
Haswellia carnea: Miers, 1884: 311. Baker, 1926: 273, 274, 279, pl. XLIX.

MATERIAL EXAMINED

Queensland Museum QM W8045, adult male, from sponge, depth 20 m, Flat Rock, North Stradbroke Island, Brisbane, Queensland (27°23·5'S, 153°33'E), M. Ready, 3 July 1979.

DESCRIPTION

ADULT MALE, 6·16 mm: (Fig. 11). *Haswellia* with dorsal surface of cephalosome and pereonites 1 to 6 smooth. Eyes large, lateral. Epistome short; surface uneven; apex narrow, acute. Dorsal process of pereonite 7 broad, scutiform, covering entire pleon and pleotelson and extending well beyond pleotelsonic apex. Process granulose with a weak, distal, median, setose keel; apex deflected ventrally. Pleotelsonic apex with a broad notch with a quadrate median tooth not reaching level of notch opening.

APPENDAGES: antennular peduncle article 1 longer than 2 and 3 together, bearing moderately pronounced acute distal projections; article 2 short; article 3 slender; 14-articled flagellum extending to level of pereonite 1. Antenna slender; 15-articled flagellum extending to pereonite 2. Mouthparts of usual sphaeromatid form, unmodified; maxillipedal palp articles 2 to 4 with pronounced setigerous lobes. Pereopods moderately robust; merus, carpus and propodus bearing inferior pads of fine setae and several long setae. Pereopod 1 with inferior margins of merus, carpus and propodus bearing long, stout spines. Penes twice as long as broad with lateral margins subparallel. Basis of pleopod 1 with three internal coupling hooks; exopod long, truncate with four externodistal teeth; endopod short, subtriangular. Pleopod 2 with exopod as in pleopod 1 but bearing 11 external teeth; endopod broad, subtriangular. Appendix masculina as long as endopod, with apex broadly rounded. Exopod of pleopod 3 with a complete, subterminal articulation. Exopod of pleopod 4 with a proximal, external squamose boss. Exopod of pleopod 5 with a subterminal, external, partial articulation. Both rami of uropod
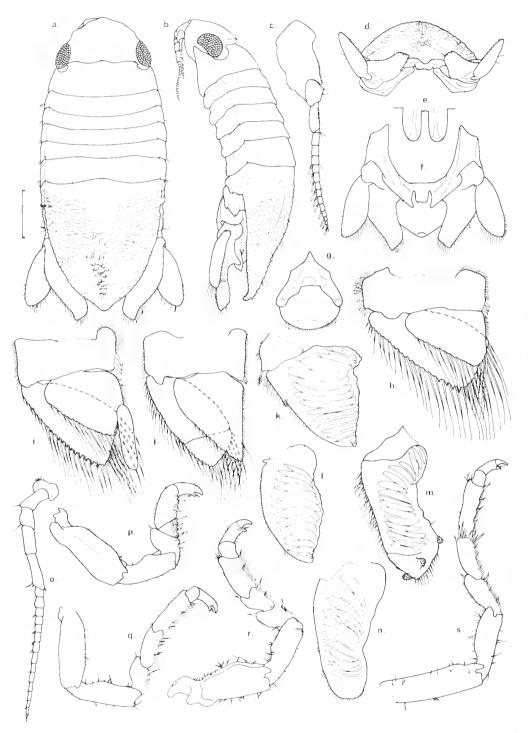
FIG. 11. *Haswellia carnea* (Haswell). Adult male (a) dorsal, (b) lateral, (c) antennule, (d) posterior, (e) penes, (f) pleotelson, ventral, (g) epistome and labrum, (h–j) pleopods 1 to 3, respectively, (k) pleopod 4, exopod, (l) pleopod 4, endopod, (m) pleopod 5, exopod, (n) pleopod 5, endopod, (o) antenna, (p–s) pereopods 1, 2, 4 and 7 respectively. Scale line representes 1 mm.

extending well beyond pleotclsonic apex, with setose margins; endopod with outer margin convex and inner margin concave. Apex truncate extending beyond subelliptical exopod.

COLOUR OF SPECIMEN IN ALCOHOL: cream with dorsal process cream-brown. Dorsal surface and ventral pereon covered with small black chromatophores.

ECOLOGY AND DISTRIBUTION

Baker (1926) reported that this species was common on the coast of New South Wales. This is the first record for Queensland where it was found in a sponge at 20 m depth.

REMARKS:

This specimen only differs from the published descriptions in lacking an acute extension on the apex of the uropodal exopod.

LITERATURE CITED

BAKER, W.H., 1908. Notes on some species of the isopod family Sphaeromidae, from the South Australian coast. *Trans. Roy. Soc. S. Australia* **32**: 138–62, Pls I–10.

1926. Species of the isopod family Sphaeromidae, from the Eastern, Southern, and Western coasts of Australia. *Trans. Roy. Soc. S. Australia* **50**: 247–79, Pls 38–53.

1929. Australian species of the isopod family Sphaeromidae (continued). *Trans. Roy. Soc. S. Australia* **52**: 49–61, Pls 1–6.

BARNARD, K.H., 1936. Isopoda collected by R.I.M.S. Investigator. *Rec. Ind. Mus.* **38**: 147–91.

BOONE, P.L., 1921. Report on the Tanaidacea and Isopoda (collected by thc Barbados-Antigua Expedition from the University of Iowa in 1918). *Univ. Iowa Stud. nat. Hist.* **9**(5): 91–8, Pl. 1.

1930. New decapod and isopod crustaccans from Gonave Bay, Haiti. *Zoologica* **12**(4): 41–53, Figs 7–10. (Not seen).

DANA, J.D., 1853. Crustacea. *United States Exploring Expedition,* **13**: 696–805.

GLYNN, P.W., 1970. A systematic study of the Sphaeromatidae (Crustacea: Isopoda) of Isla Margarita, Venezuela, with descriptions of three new species. *Mem. Soc. Cienc. Nat. La Salle* **30**(85): 5–48.

HANSEN, H.J., 1905. On the propagation, structure and classification of the family Sphaeromidae. *Quart. Journ. Microsc. Sci.* **49**(1): 69–135, Pl. 7.

HASWELL, W.A., 1881. On some new Australian marine Isopoda — Part I. *Proc. Linn. Soc. N.S.W.* **5**(4): 470–81, Pls 16–19.

1882. On some new Australian marine Isopoda — Part II. *Proc. Linn. Soc. N.S.W.* **6**: 181–96, Pls 3, 4.

1884. A revision of the Australian Isopoda. *Proc. Linn. Soc. N.S.W.* **9**(4): 1001–15, Pls 50–3.

HARRISON, K. and D.M. HOLDICH, 1982. Revision of the genera *Dynamenella, Ischyromene, Dynamenopsis* and *Cymodocella* (Crustacea: Isopoda), including a new genus and five new species of eubranchiate sphaeromatids from Queensland waters. *Journal of Crustacean Biology,* **2**(1): 84–119.

HOLDICH, D.M., 1968. A systematic revision of the genus *Dynamene* (Crustacea: Isopoda) with descriptions of thrce new species. *Publ. Staz. zool. Napoli* **36**: 401–26.

HOLDICH, D.M. and K. HARRISON, 1980a. Morphological variation in the *Serolis minuta*-group (Isopoda: Serolidae) from Australian waters. *Zool. J. Linn. Soc.* **68**: 373–86.

1980b. The isopod genus *Gnathia* Leach from Queensland waters with descriptions of nine new species. *Aust. J. Freshwat. Res.* **31**: 215–40.

1980c. The isopod genus *Dynamene* from Australian waters, with description of a new species from coral reefs. *Mem. Qd Mus.* **20**(1): 163–70.

1981a. Platybranch sphaeromatids (Crustacea: Isopoda) from the Australian region with description of a new genus. *Rec. Aust. Mus.* **33**(12): 617–43.

1981b. The sphaeromatid isopod genus *Sphaeromopsis* Holdich and Jones in African, Australian and South American waters. *Crustaceana* **41**(3): 286–300.

HOLDICH, D.M., K. HARRISON, and N.L. BRUCE, 1981. Cirolanid isopod crustaceans from the Townsville region of Queensland, Australia, with descriptions of six new species. *J. nat. Hist.* **15**: 555–605.

HOLMES, S.J., 1904. Remarks on the sexes of sphaeromids with a description of a new species of *Dynamene*. *Calif. Acad. Sci. Proc.*, Ser. 3. *Zool.* **3**: 296–306, Pl. 34.

MENZIES, R.J., 1962. The marine isopod fauna of Bahia de San Quintin, Baja California, Mexico. *Pac. Naturalist* **3**(11): 337–48.

MENZIES, R.J. and D. FRANKENBERG, 1966. 'Handbook of the Common Marine isopod Crustacea of Georgia.' (University of Georgia Press: Athens).

MENZIES, R.J. and P.W. GLYNN, 1968. The common marine isopod Crustacea of Puerto Rico. *Stud. Fauna Curaçao* **27**: 1–133.

MIERS, E.J., 1884. Crustacea *in* 'Report of the Zoological Collections made in the Indo-Pacific Ocean During the Voyage of H.M.S. "Alert" 1881-1882.' (British Museun (Natural History): London).

MILLER, M.A., 1968. Isopoda and Tanaidacea from buoys in coastal waters of the continental United States, Hawaii, and the Bahamas (Crustacea). *Proc. Unit. Stat. Nat. Mus.* **125** (3652): 1–53.

MILNE-EDWARDS, H., 1840. 'Histoire Naturelle des Crustacés,' 3. (Librairie Encyclopedique de Roret: Paris).

NAYLOR, E., 1966. Port Phillip Bay Survey 1957–1963. Isopoda. *Mem. Nat. Mus. Vict.* **27**: 183–98, 377–84, Chart 1.

NIERSTRASZ, H.F., 1931. Die Isopoden der Siboga-Expedition. 3. Isopoda Genuina. 2. Flabellifera. *In* Weber, M., *Siboga-Expedite. No.* **114** (Monogr. **32c**): 123–233.

PILLAI, N.K., 1954. A preliminary note on the Tanaidacea and Isopoda of Travancore. *Bull. Res. Inst. Univ. Travancore,* **3**: 1–23.

PIRES, A.M.S., 1980. *Sergiella angra,* a new genus and species of Sphaeromatidae (Isopoda) from Brazil. *Crustaceana,* **38**(2): 212–8.

1981. *Sergiella angra* Pires, 1980, a junior synonym of *Paracerceis sculpta* (Holmes, 1904) (Isopoda, Sphaeromatidae). *Crustaceana* **41**(2): 219–20.

RICHARDSON, H., 1899. Key to the isopods of the Pacific coast of North America, with descriptions of twenty-two new species. *Proc. Unit. Stat. Nat. Mus.* **21**: 815–69.

1905. A monograph on the isopods of North America. *Bull. U. S. Nat. Mus.* **54**: 1–727.

SAY, T., 1818. An account of the Crustacea of the United States (cont.). Description of three new species of the genus *Naesa. Journ. Acad. Nat. Sci. Philadelphia* **1**(2): 482–5.

SCHULTZ, G.A., 1969. 'How to know the marine isopod crustaceans.' (Wm C. Brown Company: Dubuque, Iowa).

SCHULTZ, G.A. and L.R. McCLOSKEY, 1967. Isopod crustaceans from the coral *Oculina arbuscula* Verrill. *J. Elisha Mitchell Scientific Soc.* **83**(2): 103–13.

SEED, W.F. 1973. Pearson Island Expedition 1969.–11. Crustacea: Isopoda. *Trans. Roy. Soc. S. Austr.* **97**(3): 207–21.

STEBBING, T.R.R., 1905. Report on the Isopoda collected by Prof. Herdman in Ceylon in 1902. *Report on the Pearl Oyster Fisheries of the Gulf of Manaar. Rep. No.* **23**: 1–64.

VANHÖFFEN, E., 1914. Die Isopoden der Deutschen Südpolar-Expedition, 1901–1903. *Deutsche Südpolar-Expedition* 1901–03, **15** *Zoologie* 7(4): 447–598.

THE GENUS *DYNOIDES* BARNARD, 1914 (CRUSTACEA: ISOPODA: SPHAEROMATIDEA) FROM EASTERN AUSTRALIA, WITH DESCRIPTION OF NEW SPECIES.

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ABSTRACT

The type of material of *Dynoides barnardi* is redescribed and figures given together with figures from new non-type material. *Dynoides viridis* sp. nov. from the Great Barrier Reef is described.

INTRODUCTION

One of the major early contributors to knowledge of the Australian isopod fauna was W.H. Baker who published a series of papers dealing exclusively with the family Sphaeromatidae (Baker, 1908, 1910, 1911, 1926, 1928). In the last of these works he described the then second known species of the genus *Dynoides*, and naming it after the founder of the genus K.H. Barnard called it *Dynoides barnardi*. Since that time five other species have been described. Bruce (1980) lists these species and provided a current description of the genus.

The present paper describes a new species from Heron Island, Great Barrier Reef, and provides a redescription of *Dynoides barnardi*. Type material has been lodged at the Queensland Museum (QM), Brisbane, and at the Australian Museum (AM), Sydney.

TAXONOMY

GENUS *DYNOIDES* BARNARD

Dynoides Barnard, 1914: 407; Nierstrasz, 1931: 198; Loyola e Silva, 1960: 91; Kussakin, 1979: 432; Bruce, 1980: 199.
Paradynoides Loyola e Silva, 1960: 101.
Dynoidella Pillai, 1965: 78.
Dynoidella Nishimura, 1976: 275 (*non* Pillai, 1965).

REMARKS. Bruce (1980) gave a diagnosis for the genus, with which the present material agrees. Comparison of the species dealt with here to other members of the genus revealed that the appendages differ only in minor ways.

The similarity of the appendages between species of the genus can be seen by comparison of the drawings given by Bruce (1980, and here), Kussakin (1979), Loyola e Silva (1960) and Pillai (1965). Separation of the males is best achieved by the differences in pleon and pleotelson morphology. The separation of females is still problematic, but it seems likely that these may be most easily separated by differences in colouration (Bruce, 1980).

A character useful in aiding identification of the genus is the strongly reflexed appendix masculina.

DYNOIDES BARNARDI BAKER, 1928 (FIGS. 1, 2)

Dynoides barnardi Baker, 1928: 56, pl. VI, fig. 5–7; Nierstrasz, 1931: 198.

MATERIAL. 2 ♂, Syntypes, (4·5 mm, 4·8 mm) (A.M. Reg. No. P. 8948). Glebe Is., E side, Berth 14, Port Jackson, N.S.W. Not attacking timber, collected from surface growth, 20.vii.1927. 1 ♂ Syntype (5·5 mm) (AM Reg. no. P9086), Goat Is., Port Jackson, N.S.W. Submerged timber (oregon), test piece 14.x.1927. Coll. F.A. McNeill.
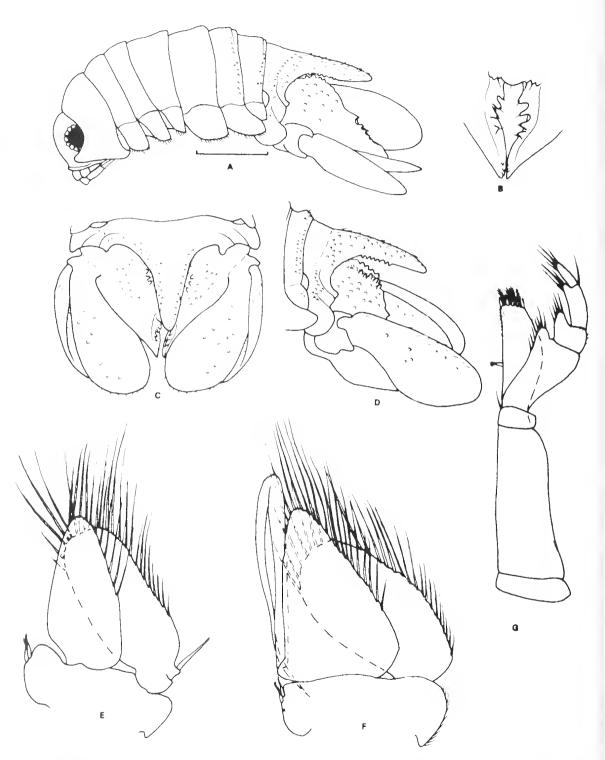
FIG. 1. *noides barnardi*. (a–c) syntype, 4·6 mm, (d–g) syntype, A.M. P8948 (a) lateral view, (b) pleotelsonic sinus, (c) dorsal view, pleotelson, (d) lateral view, pleotelson, (e) pleopod 1, (f) pleopod 2, (g) maxilliped. Scale line represents 1·0 mm (setules omitted).

2 ♂ (5·5 mm, immature 5·3 mm) (QM Reg. no. W8563) Sydney, N.S.W. November 1979. Coll. N. Svennivig.

TYPE LOCALITY. Port Jackson, New South Wales, Australia.

DESCRIPTION. ADULT MALE. Body with subparallel sides, about twice as long as broad. Anterior margin of cephalon with carina. Clypeus with anterior margin truncate, posterolateral margins produced posteriorly with extremites truncate. Pereonite 1 about twice as long as pereonite 2, pereonites 2–5 becoming progressively longer; pereonite 6 shorter than 5, and 7 shorter than 6; dorsal surface of posterior margins of pereonnites 4–7 raised, and those of pereonites 6 and 7 with tubercles. Coxal plates of pereonite 6 extending to posterior margin of pereonite 7. Pleon with large median dorsal process extending beyond origin of pleoteelsonic sinus, dorsal surface of which has numerous tubercles and setae; process has ventral lateral margins each with row of distinct tubercles. Pleotelson with dorsal surface in the form of bilobed dome, numerous small tubercles, and two rows of large distinct tubercles opposing those of the pleonal process. Pleotelsonic sinus with posterior borders almost touching, small denticles on each side; lateral margins with 4 inwardly directed lobes, each with single simple seta; anterior with inwardly projecting lobe with two simple setae on either side.

Antennular peduncle with articles 1 and 2 robust, article 2 half as long as 1; peduncular article 3 slender, 1·5 times as long as article 2; flagellum of 10 articles, all but the first bearing a single aesthetasc. Antenna with peduncular article 1 very short, articles 2 and 4 subequal in length and longer than article 3 which is half as long as article 5; flagellum composed of 16 articles.

Mouthparts. Not differing significantly from other members of the genus.

Pereopods all ambulatory. Pereopod 1 more robust than and shorter than others; superior margin of all articles except carpus with short setae and spines; superior margin of ischium not markedly angular, merus with superior distal angle produced, overreaching carpus, and provided with two large spines. Pereopod 7 slender, all articles elongate; merus with superior distal angle slightly expanded, subequal in length to carpus; propodus and ischium subequal in length.

Penes similar to other species of genus.

Pleopods and appendix masculina not differing noticeably from other members of genus.

Uropods broad, both rami with marginal setae; lateral margin of exopod folded over, dorsal and ventral surface with scattered tubercles; endopod extends beyond apex of telson by one third of its length.

FEMALE. Not known.

SIZE. Largest specimen, 5·5 mm.

COLOUR. Mottled, with khaki overlaying tan coloured ground. In alcohol coolour fades to a pale brown.

REMARKS. The character which best distinguishes this species from all others in the genus is the presence of the two rows of distinct tubercles on the dorsal surface of the pleotelson, and the two rows of tubercles on the ventral surface of the pleonal process which oppose these. The pleonal process itself is rather longer than those of other species, and the clypeus is distinctive in having nearly straight lateral margins.

Dynoides dentisinus Shen, 1929 is distinguished by the far shorter pleonal process which lacks the characteristic tubercles of *D. barnardi*, and also by having the apex of the clypeus more strongly produced.

DYNOIDES VIRIDIS, SP. NOV. (FIGS. 3, 4)

MATERIAL. 3 ♂ (4·4, 3·4, 2·8 mm), 2 ♀ (3·6 ovigerous, 3·0 mm), 4 juveniles (2·8–3·0 mm). North East reef crest, boulder zone, Heron Island, Capricorn Group, Great Barrier Reef. 17.i.1979. Coll. N.L. Bruce.

TYPES. Holotype. ♂ 4·4 mm QM Reg. no. W8522 Allotype. 3·6 mm QM Reg. no. W8523 Additional paratypes. 2 juv. QM Reg. no. W8524, 2 juv. QM Reg no. P30994

TYPE LOCALITY. Heron Island, Great Barrier Reef, Australia.
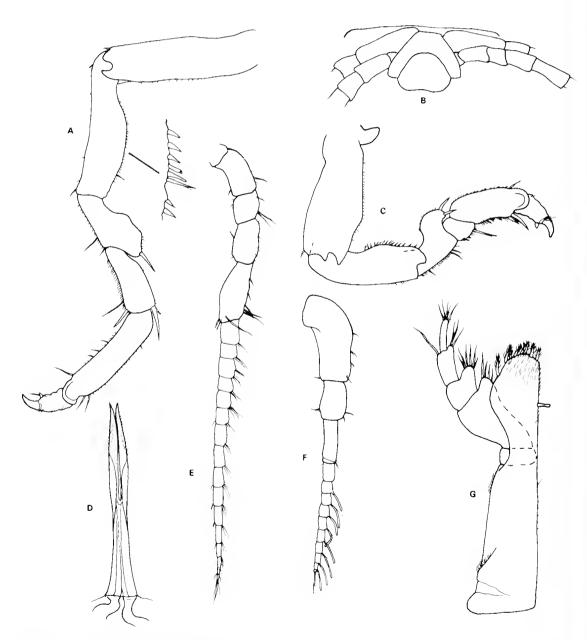
DESCRIPTION. ADULT MALE. Lateral margins of pereon sub-parallel in dorsal view, 2·5 times as long as greatest width. Anterior margin of cephalon with carina. Frontal lamina with anterior margin truncate, lateral margins backwardly directed with extremities truncate. Pereonite 1 about half as long again as pereonite 2, pereonites 2–6 subequal in length, pereonite 7 slightly shorter than 6. Dorsal surface of pereon with few setae or tubercles. Coxal plates of pereonite 6 not extending to posterior of pereonite 7. Pleon with medial dorsal process, not extending over pleotelsonic sinus, with moderate number of

small tubercles on lateral margins. Pleotelson with dorsal surface in form of bilobed dome, dorsal surface with scattered small tubercles. Pleotelsonic sinus with posterior part of sinus walls sub-parallel, 3–4 small spines projecting into sinus; anterior lobe with few small setae.

Antennule with peduncular articles 1 and 2 robust, article 3 slender, peduncular article 2 half as long as 3; flagellum composed of 11 articles. Antenna with peduncular article 1 very short, articles 2 and 4 subequal in length longer than peduncular article 3, but shorter than article 5; flagellum composed of 15 articles.

Mouthparts are similar to other species of the genus. Pereopods all ambulatory. Pereopod 1 shorter, more robust than others; basis and

2 *Dynoides barnardi* (W8563). (a) pereopod 7, (b) epistomal region, (c) pereopod 1, (d) penes, (e) antenna, (f) antennule, (g) maxilliped (setules omitted).
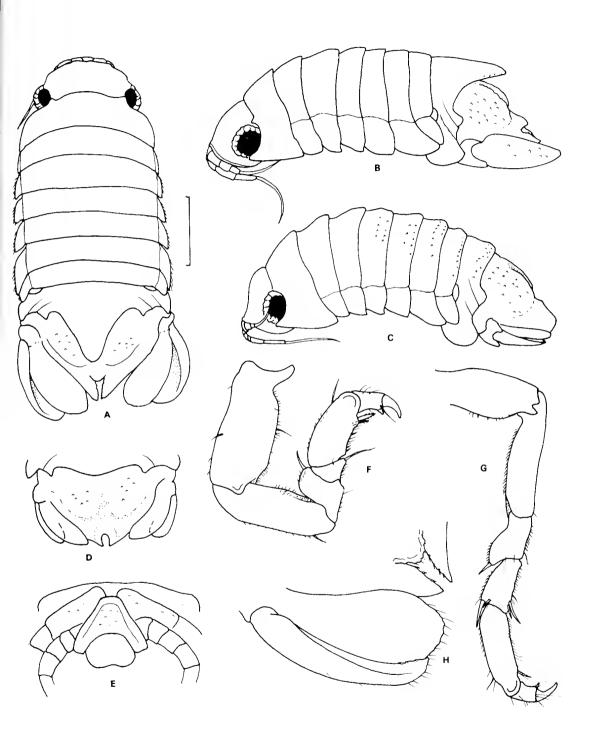
FIG. 3 *Dynoides viridis* sp. nov. holotype. (a) dorsal view, (b) lateral view, (e) clypeal region, (h) uropod and pleotelson sinus.
Allotype. (c) lateral view, (d) dorsal view, pleotelson. Paratype. (f) pereopod 1, (g) pereopod 7. Scale line represents 1·0 mm (setules omitted).

ischium equal in length, merus with superior distal angle overriding carpus; superior margins of all articles except carpus with short setae and spines. Pereopod 7 with all articles elongate; merus with superior distal margin produced; superior margins of all articles and inferior margins of merus, carpus and propodus with small spines and setae.

Penes similar to other members of genus.

Pleopods and appendix masculina not differing from other species of genus.

Uropods broad, lamellar, ventral surface with few scattered tubercles; endopod extending beyond apex of telson by one fifth of its length, both rami with marginal setae.

FEMALE. Generally similar to male, but pleon lacks dorsal process, has fewer tubercles, while the telsonic sinus is a simple u-shaped opening lacking spines, setae and the anterior lobe. The uropods do not extend beyond the pleotelson. Brood pouch formed by a series of 5 membranous plates overlapping at the midline.

COLOUR. Dorsal surface is a bright green, which fades to white in alcohol.

SIZE. Smallest recognizable adult, 3·0 mm; largest ovigerous female 3·5 mm.

ETYMOLOGY: Specific name is derived from the Latin word *viridis* meaning green, and alludes to the colouring of the live animals.

REMARKS. This small species is separated from the only other Australian species *(D. barnardi)* by differences in pleotelson morphology. *Dynoides dentisinus* Shen, from Japan and China differs in that the walls of the telsonic sinus are convergent. The briefly figured *Dynoides serratisinus* Barnard, 1914 differs in having the uropod endopod bearing a truncate posterior margin, more markedly serrate walls to the pleotelsonic sinus and the frontal lamina with the anterior margin rounded.

DISTRIBUTION. Known only from the type locality.
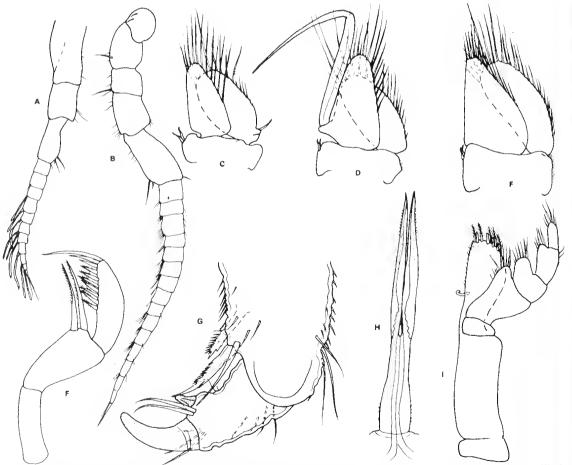
FIG. 4 *Dynoides viridis* sp. nov., paratype. (a) antennule, (b) antenna, (c–e) pleopods 1–3 respectively, (f) mandibular palp, (g) dactyl, pereopod 1, (h) penes, (i) maxilliped (setules omitted).

HABITAT

The specimens of *Dynoides barnardi* described by Baker (1928) were all taken from pieces of submerged timber, and were apparently epifaunal. The present specimens were taken from the massed calcareous tubes of the polychaete *Galeolaeria caespitosa* Lamarck, 1818, a habitat similar to that from which *D. dentisinus* has been taken in Japan (Bruce, 1980). All the specimens of *Dynoides viridis* were taken from a single intertidal boulder of dead coral rock on the reef crest at the exposed north eastern tip of Heron Island. The green colour of the animals suggest that they are probably epifaunal, because their colour resembles that of the algal turf on the coral rock.

ACKNOWLEDGEMENTS

LITERATURE CITED

BAKER, W.M., 1908. Notes on some species of the isopod family Sphaeromidae from the South Australian coast. *Trans. Proc. R. Soc. S. Aust.* **32**: 138–62.

1910. Notes on some species of the isopod family Sphacromidae from the South Australian coast. Part 11. *Trans. R. Soc. S. Aust.* **34**: 75–888.

1911. Notes on some species of the isopod family Sphaeromidae from southern Australian seas. Part III. *Trans. R. Soc. S. Aust.* **35**: 89–93.

1926. Species of the isopod family Sphaeromidae from the eastern, southern and western coasts of Australia. *Trans. R. Soc. S. Aust.* **50**: 247–79.

1928. Australian species of the isopod family Sphaeromidae (continued). *Trans. R. Soc. S. Aust.* **52**: 49–61.

BARNARD, K.H., 1914. Contributions to the crustacean fauna of South Africa — 3. Additions to the Marine Isopoda, with notes on some previously incompletely known species. *Ann. S. Afr. Mus.* **10**: 325a–58a, 359–422.

BRUCE, N.L., 1980. The systematics of some Japanese marine isopod Crustacea (Fam. Sphaeromatidae) of the genera *Dynoides* Barnard, 1914 and *Cymodocella* Pfeffer, 1887, with description of two new species. *Crustaceana* **38**: 199–211.

KUSSAKIN, O.G., 1979. 'Marine and Brackish Water Isopod Crustacea. Suborder Flabellifera.' Leningrad Acad. Science: pp. 470.

LAMARCK, J.B.P.A. DE M. DE., 1818. 'Histoire Naturelle des Animaux sans Vertebres,' 5. (Paris) 1–618.

LOYOLA E SILVA, J., 1960. Sphaeromatidea do littoral Brasiliero (Isopoda — Crustacea). *Bolm. Univ. Parana, Zoologica.* **4**: 1–182.

NIERSTRASZ, H.F., 1931. Die Isopoden Der Siboga Expedition 111. Isopoda Genuina 11. Flabellifera. *Siboga Exped., Monogr.* **32C**, Livre 114: 123–233.

NISHIMURA, S., 1976. *Dynoidella conchicola* gen. et sp. nov. (Isopoda : Sphaeromatidae), from Japan with a note on its association with intertidal snails. *Publ. Seto. Mar. Biol. Lab.* **23**: 275–82.

PILLAI, N.K., 1965. Isopods of the family Sphaeromidae from the littoral waters of South India. *Crustaceana* **9**: 75–89.

SHEN, C.J., 1929. Description of a new isopod, *Dynoides dentisinus* from the coast of North China. *Bull. Fan. Mem. Inst. Biol.* **1**: 63–78.

PYCNOGONIDA OF THE CALLIOPE RIVER & AUCKLAND CREEK, QUEENSLAND

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ABSTRACT

Nine identifiable species of pycnogonid are recorded from the lower reaches of the Calliope River and Auckland Creek. The collection includes two new species *(Hemichela longiunguis* and *Anoplodactylus calliopus),* and the ranges of three species are extended, including one new record for Australian waters. *Anoplodactylus pulcher* is synonomized with *Anoplodactylus tubiferus* and *Endeis picta* is synonomized with *Endeis straughani.* The genus *Metapallene* is synonomized with the genus *Propallene.* Cement glands are recorded for the first time in *Endeis straughani* and *Anoplodactylus simplex.* The holotype of *Anoplodactylus haswelli* has been re-examined in an attempt to clarify uncertain morphological characters.

INTRODUCTION

This paper is based on collections made by the Queensland Electricity Generating Board during an environmental study carried out before and after The Gladstone Power Station was commissioned in September 1976. All specimens represented were collected by Van Veen grab in very shallow water (depth 0·8 m. – 9·0 m).

The following species are represented:

FAMILY CALLIPALLENIDAE: *Parapallene australiensis* (Hoek 1881); *Propallene saengeri* Staples, 1979; *Pigrogromitus timsanus* Calman, 1927 (new record for Australia).

FAMILY PHOXICHILIDIIDAE: *Anoplodactylus tubiferus* (Haswell 1884) range extension; synonymized with *A. pulcher* Carpenter, 1907; *Anoplodactylus calliopus* sp. nov.; *Anoplodactylus simplex* Clark, 1963 (range extension); *Anoplodactylus* sp. (juveniles).

FAMILY ENDEIDAE: *Endeis straughani* Clark, 1970.

FAMILY AMMOTHEIDAE: *Hemichela longiunguis* sp. nov.

FAMILY COLOSSENDEIDAE: *Rhopalorhynchus tenuissimum* (Haswell, 1884).

The present collection has increased the number of pycnogonid species recorded in Queensland from twenty-two to twenty-eight. This includes *Propallene saengeri* Staples, 1979 described earlier from the same collection.

Sampling stations were located in the cooling water outfall canal and at each of eleven transects selected along the River and Creeks. These transects extended to a distance of 15·1 km upstream. The location of the transects (1–11) and the cooling water outfall canal (cw) are shown in Fig. 1. Primary data relating to each individual transect is provided by Saenger et al., 1980. The second number in each River and Creek station code identifies the particular transect. Cooling water outfall canal stations are designated cw.

Institutions in which material has been lodged are referred to by the following abbreviations: National Museum of Victoria (NMV); Queensland Museum (QM); Institute of Taxonomic Zoology (Zoologisch Museum, Amsterdam) (ZMA); Zoological Museum, University of Copenhagen (ZMUC); National Museum of Natural History, Washington, D.C. (USNM); National Museum, Wellington (NMW). Comparative material has also been lodged with the Queensland Electricity Board (QEGB).

Family CALLIPALLENIADAE Hilton 1942
Genus *Parapallene* Carpenter, 1892
Parapallene australiensis (Hoek, 1881)

SYNONOMY:

Pallene australiensis Hoek, 1881, pp 76–78, pl. X1, figs 1–7 (in part). Haswell, 1884, p. 1022.

Parapallene australiensis Carpenter, 1892, p. 553. Loman, 1908, p. 48. Calman 1937, pp. 530–532 (redescr. of types). Stock, 1954, p. 50, fig. 24 d–e; 1973a, p. 119. Clark, 1963 pp. 25–26. Child 1975, p. 12.
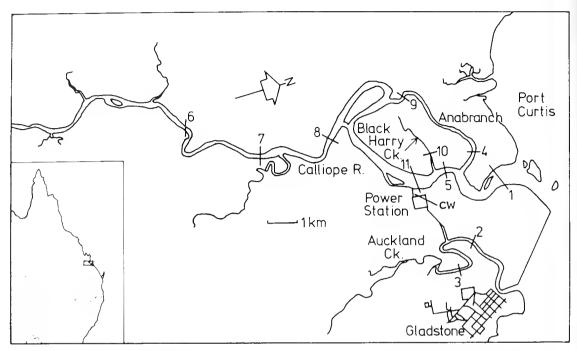
FIG. 1. Map of study area showing locations of transects 1–11 and cooling water outfall (cw) (after Saenger et al., 1980).

MATERIAL EXAMINED: Calliope R., cooling water screens 21.viii.1977, 1 ♂ QM S895.

DISTRIBUTION: Eastern and southern coasts of Australia.

DISCUSSION:
This solitary specimen is subadult. I have little doubt that the 'true articulation' or 'transverse fold of cuticle' in front of the ocular tubercle as noted by Hoek (1881, p. 76) and Calman (1937, p. 531) respectively, has resulted from the crimping of the cuticle due to flattening of the arched body under a glass slide. I am also of the opinion that the cuticular fold described in several other members of the genus, notably *P. nierstraszi* Loman, 1908, *P. longipes* Calman, 1938 and *P. challengeri* Calman, 1937b has resulted in a similar manner. The eye tubercle in the present specimen has a bifurcated apex. Examination of several specimens from Westernport Bay Victoria, indicates that the shape of the eye tubercle is a variable character ranging from acutely conical to distinctly bifurcate at the apex.

Genus *Propallene* Schimkewitch, 1909
Propallene saengeri Staples, 1979

SYNONYMY:
Propallene saengeri Staples, 1979, pp. 90–93 fig. 2D, fig. 4A–L.
MATERIAL EXAMINED: Calliope R., Stns. 22/10/3, 13/5/5, 1 ♂ (ovig.) 1 ♀ (gav.) ZMA Pa. 2889; 15/1/5, 17/5/1, 1 ♂ 1 ♀ (grav.) ZMUC; 21/11/1, 3 ♂ (2 ovig.) 2 ♀ (grav.) NMNZ Pyc 50; 8/11/5, 15/4/1, 18/11/1, 22/7/5, 22/1/1, 22/10/3, 22/9/5, 8/9/5, 19/9/5, 5 ♂ (4 ovig.) 12 ♀ (11 grav.) NMV K71 Auckland Ck, Stns. 18/3/3, 18/2/2, 15/2/1, 1 ♂ (ovig.) 2 ♀ (grav.) NMV K72; 8/2/2, 1 ♂ (ovig.) 1 ♀ (grav.) QEGB.
DISTRIBUTION: Central Queensland.
DISCUSSION:
The genera *Metapallene* Schimkewitsch, 1909 and *Propallene* have been distinguished principally by the presence of one or two palp segments in the male. Recently it has been demonstrated that in subadult forms the palps of *Propallene* are one-segmented and not until maturity do the second segments become evident. (Staples, 1979, fig. 1F; Nakamura 1981, p. 57, fig. 17). *Pallene longiceps* Bohm, 1879 was correctly assigned to the genus *Propallene* by Schimkewitsch (1909).

Schimkewitsch (1909) also erected the genus *Metapallene* and named *Pallene languida* Hoek, 1881 as the type species. Re-examination of Hoek's specimen now shows that *Metapallene* was founded on a subadult *Propallene*. Accordingly I propose that *Metapallene* be synonomized with *Propallene*. Another genus, *Pallenoides* Stock, 1951 may also have been based on a subadult male or more likely, a female *Propallene*. The structure of the oviger spines and variation in their shape (proximal and distal spines dissimilar) distinguishes the type species *P. magnicollis* from other members of the genus and places it in agreement with the diagnosis of the genus *Propallene*. The sex of the type specimen is in doubt (Stock, 1955 pp. 226-227). The absence of a distal apophysis on the fifth oviger segment combined with the absence of palps would suggest it to be female.

Genus *Pigrogromitus* Calman, 1927
Pigrogromitus timsanus Calman, 1927
Fig. 2 G–J

SYNONOMY:

Pigrogromitus timsanus Calman, 1927, pp. 408–410 fig. 104 A–F. Hedgpeth, 1948, pp. 214–216, fig. 23. Stock, 1968a, p. 46; 1975 pp. 1015–1016. Lipkin and Safriel, 1971, p.9. Arnaud, 1972, pp. 159–160.

Clotenopsa prima Hilton, 1942, pp. 52–58, fig. 8.

MATERIAL EXAMINED: Calliope R., Stns. 11/11/1, cw/4, 1 ♂ 1 ♀, QM S897; 12/1/1, 33/cw/3, 1 ♂ 1 ♀ (grav.) USNM 184170; Oct. 1976, cw/3, 2 ♂ (1 ovig.), 2 ♀ (1 grav.), ZMUC; 27/cw/1, 1 ♂ 1 ♀, ZMA Pa. 2888; 25/cw/2, 1 ♂ 1 ♀ 1 juv., NMNZ Pyc51; 18/4/5, 45/cw/1, 1 ♂ (ovig.) 1 ♀ (grav), QEGB; 21/11/1, 18/5/1, 18/11/1, 21/8/3, 26/cw/2, 28/cw/2, 32/cw/2, 33/cw/2, 10/cw/3, 14/cw/3; 24/cw/3, 30/cw/3, 31/cw/3, 30/cw/4, 43/cw/4, 15/cw/5, 13/cw/4, 25/cw/5, 27/cw/5, 33/cw/5, 42/cw/5, 46/cw/5, cw/11/1, cw/11/2, cw/12/2, cw/23/5, 26/cw/1, cw/12/5, 31/cw/4, 26/cw/5, 13 ♂ (1 ovig.) 29 ♀ (7 grav.) 22 juv. NMV K73. Other material: Panama, Caribbean. Galeta I., intertidal, Laurencia Sample 6 Col. STRI Survey Group. 1 ♂ (ovig.) 1.iii.1971 (USNM 154460); Panama, Caribbean: Galeta 1., Intertidal, Laurencia Sample 7 Coll. STRI survey group. 1 ♀ 1 juv., 2.iii.1971 (USNM 154461).

DISTRIBUTION: Circumtropical.

DISCUSSION:

The present material represents the first record of this species from Australian waters. In comparison with Calman's (1927, fig. 104A) illustration of the male holotype the Queensland specimens have reduced median trunk tubercles and are more compact with lateral processes touching or almost touching (rarely diverging) throughout their length. The sixth segment of the male oviger bears a strong spine on its outer margin, which although illustrated by Calman (fig. 104 E), is not mentioned in the text. The specimens from Queensland and from Galeta I. are very similar. Several juveniles were firmly attached to sea anemones with their proboscides inserted into the host tissue.

Family PHOXICHILIDIIDAE Sars, 1891
Genus *Anopodactylus* Wilson, 1878
Anoplodactylus tubiferus (Haswell, 1884)
Fig. 2 C–F

SYNONOMY:

Phoxichilidium tubiferum Haswell, 1884, p. 1032, pl. 57, figs 1–5. Whitelegge, 1889, p. 223.

Anoplodactylus tubiferus Cole, 1904a, p. 288. Loman, 1908, p. 72. Flynn, 1919b, pp. 79–81, pl. XX, figs. 12–14, pl. XXI, fig. 15. Williams, 1941, p. 35. Clark, 1963, p. 49; Stock, 1979, p. 158.

Anoplodactylus pulcher Carpenter, 1907, p. 97–98, pl. 12, figs. 13–19 (new synonomy); Stock, 1954b, p. 84; 1965a: 29, fig. 45; 1968b: 49; 1973b: 92; 1979, p. 158. Arnaud, 1973a, p. 957.

Anoplodactylus stylops Loman, 1908, p. 71, pl. 11, figs. 20–24.

MATERIAL EXAMINED: Calliope R., Stns. 15/9/3, 15/1/5, 1 ♂ (ovig.) 1 ♀ (grav.) QEGB; 22/7/5, 11/11/1, 1 ♂ 1 ♀ ZMA Pa. 2890; 8/9/5, 16/1/2, 1 ♂ (ovig.) 1 ♀ ZMUC; 4/9/4, 19/6/2, 1 ♂ 1 ♀ (grav.) USNM 184893; 22/7/5, 1 ♂ (ovig.) NMNZ Pyc45; 14/1/2, 1 ♀ (grav.) NMNZ Pyc46; 11/4/4, 8/4/1, 1 ♂ 1 ♀ QM896; 11/11/2, 8/5/1, 8/1/2, 12/1/5, 22/7/5, 23/1/2, 18/10/2, 22/10/2, 8/9/2, 22/4/2, 19/9/2, cw/5/4, cw/5/1, cw/4/3, 5 ♂ (1 juv.) 15 ♀ (1 grav. 1 juv.) NMV K74 Auckland Ck, 17/2/2, 18/3/3, 15/2/2, 12/2/3, 8/2/2, 16/2/3, 22/3/1, 11/3/4, 19/3/2, 17/2/3, 11 ♂ (1 ovig.) 4 ♀ (2 grav.) NMV K75. Other material: Reef at Carnac 1., Western Australia, in red algae, 21.iii.1972, 1 ♂, coll. N. Coleman ZMA Pa. 2028; Persian Gulf; 25° 55'N, 50° 16'E, trawl, bottom, marl and shell, 13 m. 6.ix.1956, 1 ♀ coll. C. E. Dawson, St. 4 ZMA Pa. 1718; Anton Bruun, Cruise 7, St. 363W,

Mozambique Channel, 23° 19'S, 43° 36'E, trawl. 91–73 m. 6.viii.1964, 2 ♂ ZMA Pa. 1751; Madagascar: region of Fort Dauphin, 2½ miles W. of Pointe Itaperina, trawled in 50 m. bottom shelly sand, 19.x.1958, 1 ♂ Coll. Dr. A. Crosnier, nr. ch–2. ZMA Pa. 1600. Syntype: *A. stylops* Loman, 1908, Banda Sea Indonesia 1 ♀ USNM 128212.
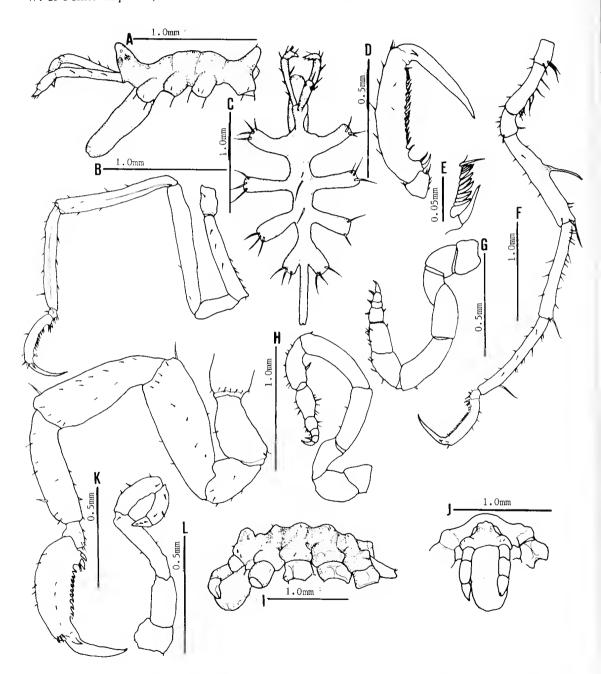
FIG. 2. *Anoplodactylus simplex* A, Trunk, lateral view, female; B, Leg 3, male. *Anoplodactylus tubiferus* C, Trunk of male, dorsal; D, Distal leg segments, male; E, Distal spines propodal sole, male; F, Leg 3, male. *Pigrogromitus timsanus* G, Oviger, female; H, Oviger, male I, Trunk, lateral view, male; J, Cephalic region, anterior view, male. *Anoplodactylus haswelli*, K, Leg 3, male, holotype; L Oviger male, holotype.

DISTRIBUTION: Madagascar, Mozambique Channel, Persian Gulf, Paumben (India), Maldive Is. (Indian Ocean) Carnac I. (W. Australia), Banda Sea (Indonesia) and the east coast of Australia.

DISCUSSION:

The Queensland specimens are smaller and the distal processes on the femora and first tibiae are not as well developed as those from elsewhere, otherwise there is little to distinguish the specimens. The present material is closest to the specimens from the Mozambique Channel, particularly in the shape of the propodus. The number of propodal sole spines is age dependent and in the Queensland material ranges from five in subadults to 22 in adults. The propodal sole bears a distal group of approximately 12 closely set spinules which may be spiniform or peg-shaped. As far as I am aware only two other species, *A. eroticus* Stock, 1968b and *A. coxalis* Stock, 1968b possess a similar group of spinules. The number of setae on the lateral processes and legs varies considerably, the Carnac I. specimen is exceptional in possessing 10–20 long setae on each lateral process. This specimen also differs from the others in having the second coxa of each leg distinctly less than twice the length of coxa three (approximately equal — distinctly longer in other material). Palps are represented by two low bulges situated proximally on the anterior margin of the first lateral process. Trunk segmentation is variable, often entirely lacking. *A. tubiferus* is such a distinctive species that I have little hesitation in synonomizing *A. pulcher* with it.

Anoplodactylus calliopus sp. nov.
(Fig. 3 A–K)

HOLOTYPE: Calliope River, Stn. 21/11/1, 4·4 m, June 1980 1 ♂ QM S898.
ALLOTYPE: Auckland Creek, Stn. 18/2/2, 2 m, July 1979 1 ♀ (grav.) QM S899.
PARATYPES: Calliope R., Stn. 21/11/1, 4·4 m, June 1980 1 ♂ 6 ♀ NMV K77, 1 ♀ NMNZ Pyc 47, 1 ♂ ZMA Pa. 2891; Stn. 21/11/2, 3·9 m June 1980 1 ♂ USNM 184894; Stn. 21/1/5, 5·6 m, June 1980, 1 ♀ (grav.) ZMA Pa. 2892. Black Harry Ck., Stn. 20/10/3, 2·7 m, March 1980 1 ♀ USNM 184895. Auckland Ck., Stn. 22/2/1, 1·3 m, Oct. 1980 1 ♂ (ovig.); Stn. 18/2/5, 1 m, July 1979, 1 ♀ (grav.) NMV K78.

DIAGNOSIS:

Anoplodoctylus with single femoral cement gland emerging through long duct; propodus with strong heel, bearing single stout spine; lamina 2/3 length of sole, preceded by conical process and recurved spine; auxiliary claws lacking. Ventral outgrowths lacking on ♀ proboscis, chela fingers denticulate.

DESCRIPTION:

TRUNK: Intersegmental lines indistinct or lacking; lateral processes touching or close together at their origins, longer in male, fourth process shorter than remainder; processes 1, 2 and 3 with low tubercle distally, tipped with a single spinule. Abdomen well developed, inclined upward at an angle of about 45°; bears small spines distally. Ocular tubercle with two lateral and one posterior apical processes; eyes four, distinctly pigmented; lateral sense organs not evident.

PROBOSCIS: stout, inserted anteroventrally on cephalon, few minute setae distally, slight swellings subterminally; mouth opening large; ventral outgrowths lacking.
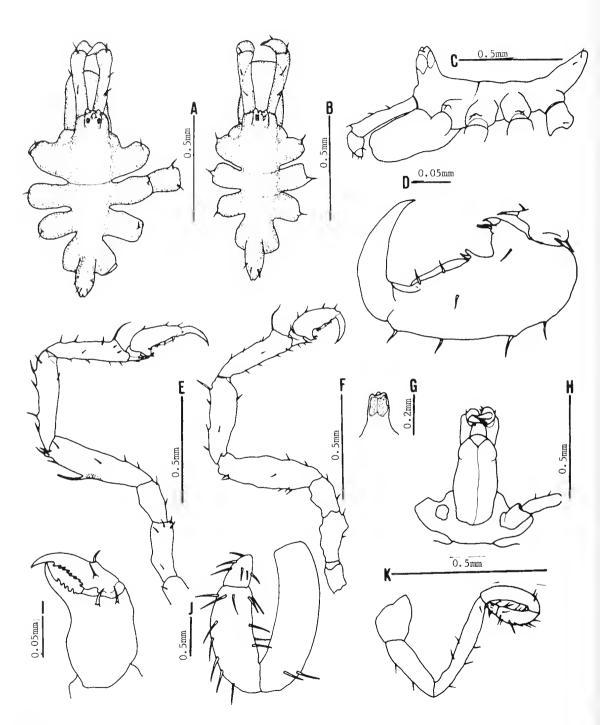
PALPS: vestigial organs not evident.

CHELIFORES: scape one-segmented, not touching at base, armed with few dorsal setae; both fingers curved, dactylus with seven–eight denticles, immovable finger with five denticles, three setae at base of dactylus, a few strong setae on palm.

OVIGER: in male only, six-segmented, segment three longest, segments five and six armed with numerous recurved setae. Measurements of oviger segments ♂ holotype (mm): 1, 0·11; 2, 0·21; 3, 0·32; 4, 0·15; 5, 0·12; 6, 0·04.

THIRD LEG: Femur the longest segment, male with cement gland on median dorsal surface, duct equal to or slightly longer than width of femur. PROPODUS: heel strong, armed with single stout spine proximally and a pair of more slender spines distally; lamina about 2/3 length of sole, preceded by obtuse conical process with recurved spine. Auxiliary claws absent. Genital pores (female) on low mound on 2nd coxae of all legs, in males pores on legs three and four only.

Measurements (mm) of ♂ holotype (those of ♀ allotype in brackets). Length of trunk (anterior margin of cephalon to tip 4th lateral process) 0·76 (0·63); length cephalon 0·31 (0·27); width across 2nd lateral processes 0·60 (0·48); length proboscis (ventral) 0·43 (0·43) greatest width proboscis 0·23 (0·22); length chelifore scape 0·30 (0·31); length abdomen 0·20 (0·19). Third leg: 1st coxa 0·14 (0·13); 2nd coxa 0·26 (0·23); 3rd coxa 0·19 (0·16); femur 0·46 (0·47); 1st tibia 0·42 (0·37); 2nd tibia 0·35 (0·34); tarsus 0·05 (0·05); propodus 0·24 (0·20); claw 0·14 (0·12); length of cement gland duct 0·11.

FIG. 3 *Anoplodactylus calliopus* sp. nov. A, Trunk, dorsal view, male; B, Trunk, dorsal view, female; C, Trunk, lateral view, female; D, Leg 3, distal segments, female; E, Leg 3, male; F, Leg 3, female; G, Eye tubercle, anterior view, female; H, Cephalic region, ventral view, male; 1, Chela, male; J, Oviger, distal segments, male; K, Oviger,

DISCUSSION:

Only *A. arescus* Marcus, 1959 shares the following combination of characters with *A. calliopus:* lateral processes close together; a strong propodal lamina; auxiliary claws absent and a femoral cement gland duct about as long as femur is wide. *A. calliopus* is distinguished from *A. arescus* by the presence of low spiniform tubercles on lateral processes 1–3 (absent in *A. arescus)* and by the shape of the propodus. In *A. calliopus* the heel is more pronounced and lacks the swelling or 'cushion' evident at the base of the heel in *A. arescus*. The lamina occupies 2/3 the length of the propodal sole and is preceded by a conical process. In *A. arescus* the lamina occupies the entire length of the sole. *A. calliopus* is another member of the *A. pygmaeus* complex of Stock (1975, p. 1075–6), a group of small compact species. Only two other members of this complex are found in Australian waters which possess a propodal lamina and lack auxiliary claws. These species are *A. minusculus* Clark, 1970 and *A. spinirostrum* Stock, 1973a. From both these species the present material differs principally in the length of the cement gland duct, the shape of the propodal heel and possession of a single stout heel spine (two in *A. minusculus, A. spinirostrum)*.

I have named this species for the Calliope River, its type locality.

Anoplodactylus haswelli (Flynn, 1918)
Fig. 2 K–L

SYNONOMY:

Halosoma haswelli Flynn, 1918 pp. 3–5 Pl. 1, figs 1–6.

Anoplodactylus haswelli Williams, 1941 p. 33–35. Clark 1963 pp. 48–49, figs 24 A–D.

HOLOTYPE: Shark I., Port Jackson; low tide amongst mussels. 1 ♂, (7 slides) AM. P4156–P4162.

DISCUSSION.

In the absence of a description of the male cement gland aperture(s) — a prime diagnostic character — it is not possible to adequately compare this species with others in the genus. Although not represented in the present collection I have re-examined the holotype in the hope of clarifying this aspect. Due to the manner in which the holotype specimen has been mounted the cement gland openings cannot be seen. However it is evident that the glands do not open through a

duct. The third leg is re-illustrated in greater detail and a complete figure of the male oviger is provided.

Anoplodactylus simplex Clark, 1963
Fig. 2 K–L, Plate 1, Figs C–D

SYNONOMY:

Anoplodactylus simplex Clark 1963 pp. 50–51, fig. 25 A–F. Stock, 1979, p. 158.

MATERIAL EXAMINED: Calliope R., Stns. 8/11/1, 1 ♂ QEGB; 18/8/1, 1 ♀ NMNZ Pyc48; 18/7/5 1 ♀ (grav.) QM S909; 8/1/5, 1 ♂ 1 ♀ USNM 184896; 8/4/1, 1 ♀ ZMUC; 17/1/2, 8/11/5, 1 ♂ 1 ♀ NMV K79. Auckland Ck., 18/2/2, 1 ♂ 1 ♀. ZMA Pa. 2893; 8/3/4, 1 ♂ QM S909; 8/2/2, 1 ♀ QEGB. Other material: Holotype, Shallow Bay, just south of Kurnell, Botany Bay, NSW. Dredged 15 ft. sand and weed. 1 ♂ (ovig.) Coll. F. McNeill and party AM P28423. Allotype, 1 ♀ AM P28422 same locality details.

DISTRIBUTION. East coast, Australia.

DISCUSSION:

Re-examination of the holotype together with the additional material now at hand reveals the presence of some 22–30 inconspicuous femoral cement glands in the male. These glands open through minute pores only evident when viewed under high magnification (Pl. 1, C–D). Distally each lateral process bears one (or two) small dorsal spines. The eye tubercle bears lateral sense organs situated above the eyes. Propodal lamina lacking.

Anoplodactylus sp.

MATERIAL EXAMINED: Calliope R., Stns. 38/cw/4, 41/cw/5, 1 ♂ (juv.) 1, protonymphon QM S902.

DISCUSSION.

I am unable to determine these species with any certainty.

Family ENDEIDAE Norman, 1908
Genus *Endeis* Philippi, 1843
Endeis straughani Clark, 1970
Fig. 5 K–M. Plate 1, Figs A–B

SYNONOMY:

Phoxichilus charybdaeus(?) Haswell, 1884.

Endeis straughani Clark, 1970: 13–15 fig. 1–5.
Endeis picta Bamber, 1979: 251–254 fig. 1 A–I.

MATERIAL EXAMINED: Calliope R., Stns. screens 8/2/80, 1 ♂ (ovig.) QM S903; 45/cw/2, 1 ♀ NMNZ Pyc52; 30/cw/2; R.B. 29.xi.1979, 4 ♂ (1 ovig., 2 juv.) 2 ♀ NMV K76. Other material: Paratypes, Northern Electrical Authority Power-house, Ross Ck., Townsville, Queensland 1 ♀ 2 ♂ 3 juv. coll. I.M. Straughan, 31.i.1967 QM S19. *Endeis picta* Bamber, Gold Coast fouling community 12.xii.1975 1 ♂ holotype. BM 1977:81:1; 2 ♀ paratypes same locality BM 1977:82:3.

DISTRIBUTION: Queensland (Australia); Ghana (W. Africa).

DISCUSSION.

Re-examination of the paratype specimens of *E. straughani* together with the additional material now at hand permits amplification of the existing description. Approximately 25–30 minute cement glands arranged mainly in a single row are situated dorsolaterally on the posterior surface of each femur in the male; toward the middle of the femur a second irregular row of approximately eight glands occurs (Pl. 1, A–B). Sixth oviger segment with inflated external surface, sometimes lobe-like, bearing three–five spinules. A similiar swelling or lobe has previously been noted in *E. mollis* (Carpenter, 1904) by Calman (1938, p. 160) and Barnard (1954, p. 131) and also on the internal surface of the sixth oviger segment in *E. flaccida* Calman, 1923 by Stock (1975, p. 1085). On its inner margin the sixth oviger segment bears two strong recurved spines. Clark (1970 p. 15) stated that genital pores in the male are situated on the third and fourth legs. I have been unable to locate the male holotype, however, in the two male paratypes before me genital pores are present on legs 2, 3 and 4. In a single instance a small pore is also present on leg 1. This pore is not situated on a low tubercle as in legs 2, 3 and 4. The number of heel spines in adults varies from three–five, and is not always constant in one specimen. Eye tubercle more acute in some specimens than in others and bears small lateral sense organs. In adults the length of the proboscis (measured ventrally) varies from 64%–83% (mean 74%) of the length of the trunk (measured from the tip of the cephalon to

the tip of the 4th lateral process). A small inconspicuous tubercle which may bear a small apical spine is situated on the neck at the base of each collar lobe. Collar lobes rounded, not meeting mid-dorsally. A few minute setae may be present mid-dorsally on trunk segments 1, 2 and 3. Eggs small, carried in a single mass wrapped around both ovigers. Sub-adults in the present material are characterised by having tibia 2 longer than the femur (femur longer in adults) and by having well developed spines on the neck, lateral processes and coxa 1 which in adults are either reduced or replaced by a blunt tubercle. After comparing the holotype and paratypes of *E. picta* Bamber, 1979 with *E. straughani* I consider them to be conspecific. The Ghana specimens are more compact and possess genital pores on all legs. In view of the variability found in the Queensland specimens and the limited material available for comparison I have not placed much reliance on these characters. I am of the opinion that several distinguishing features cited by Bamber (relatively unhirsuite propodus, porportionately smaller tarsus and more obvious cement glands) are not significant. Using Stock's key (1968b, p. 59) *E straughani* can be followed down to couplet 7a where it keys out with *E. biseriata* Stock 1968b, p. 57.

The differences between *E. straughani* and the short-spined form of *E. biseriata* are slight. Stock described the holotype of *E. biseriata* as having widely spaced lateral processes (space between 2nd and 3rd processes 0·82 mm each provided with a single spiniform projection (dorsal eminences lacking) and in having tibia 2 longer than the femur. Oviger segment 4 is longer than segment 5, a character upon which Stock (1979 p. 30) has placed some reliance. The specimens of *E. straughani* in the present collection are compact (space between 2nd and 3rd processes 0·33 mm–0·48 mm) with one or two low dorsal eminences on each process (spines absent in adults). The femur is consistently longer than tibia 2 in adult specimens and oviger segment 5 is longer than segment 4. In isolation these differences may not be particularly significant however when taken in combination I believe that the retention of *E. straughani* as an independent species may be justified.

Critical examination of all available material is required to elucidate the relationship between these species.

Family AMMOTHEIDAE Dohrn, 1881
Genus *Hemichela* Stock, 1954
Hemichela longiunguis sp. nov.
Fig. 4 A–L

HOLOTYPE: Calliope River, Stn 18/10/2, 1·3m,
July 1979, 1 ♂ (QM S900).

ALLOTYPE: Anabranch of Calliope River, Stn
8/4/2, 5·2m, Nov. 1976, 1 ♀ (grav.) QM S901.

PARATYPES: Calliope R., Stn 22/8/5, 2m, Nov
1976, 1 ♀ (grav.) (ZMUC); Stn. 21/7/5, 2·2m,
Aug. 1976, 1 ♂ (ovig). ZMA Pa. 2895; Stn.
7/1/1, 1·6m, Aug. 1976, 1 ♀ (grav.) ZMA Pa.
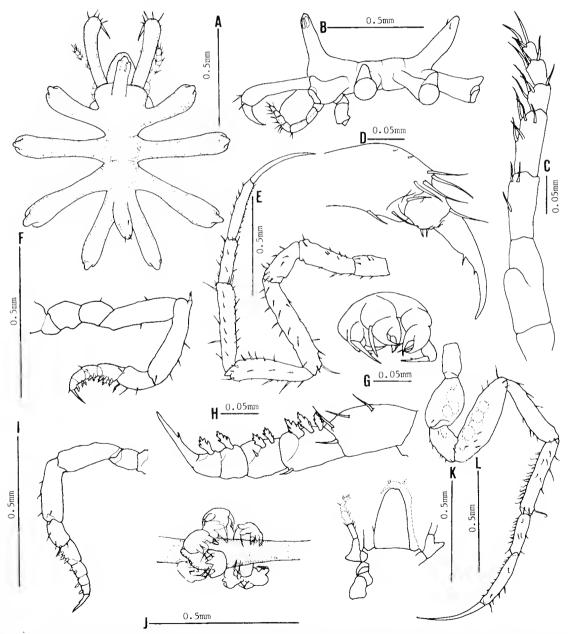
FIG. 4. *Hemichela longiunguis* sp. nov. A, Trunk, dorsal view, male; B, Trunk, lateral view, male; C, Palp, female; D, Chela, female; E, Leg 3, male; F, Oviger, male; G, Protonymphon; H, Oviger, distal segments, female; I, Oviger, female; J, Protonymphon on lateral process; K, Cephalic region, ventral, female; L, Leg 3, female.

2896; Stn. 8/8/4, 4·6 m, Nov. 1976, 1 ♀ (grav.) USNM 184897 19/11/1, 3·2m, Nov. 1979 1 ♂ (ZMUC). Anabranch of Calliope R., Stn. 22/9/3, 5·8m, Oct. 1980, 1 ♂ USNM 184898; Stn. 15/4/2, 5·2m, Oct. 1978, 1 ♀ (grav.) NMNZ Pyc 49; Stn. 22/9/5, 1·2m, Oct 1980, 1 ♂ (ovig.) 2 ♀ (grav.) NMV K81; Auckland Ck, Stn. 22/2/1, 1·3m, Oct. 1980, 1 ♂ NMV K82.

DIAGNOSIS:

Hemichela with a pronounced lateral process on each second palp segment. Terminal claw longer than propodus; chela finger with two denticles on inner margin.

DESCRIPTION:

Trunk intersegmental lines variably developed, generally indistinct or absent. Lateral processes diverging; slightly dilated, armed with a single distal tubercle, each tubercle with several minute setae. Eye tubercle slender, situated at anterior margin of cephalon, height approx. 2·5 times basal diameter, two dorsolateral papillae; eyes four, indistinct. Proboscis tapering, slightly constricted at about half its length, directed ventrally at approx. 45°. Abdomen slender, directed upwards at an angle of about 45°, armed distally with three–four small spines. Chelifore scape one-segmented, armed distally with several long setae. Chela with dactylus only, curved and bearing two denticulations on inner margin. Palm short, with few long setae.

Palps seven-segmented, segments three–seven armed with long setae, segment 2 with pronounced lateral process on the outer surface, process in female larger than male.

Measurements (mm) of palp segments ♂ holotype (those of ♀ allotype in brackets): 1, 0·05 (0·05); 2, 0·12 (0·12); 3, 0·10 (0·09); 4, 0·08 (0·07); 5, 0·04 (0·04); 6, 0·03 (0·04); 7, 0·03 (0·04).

Ovigers ten-segmented; segment 5 longest; in ♂ bears reversed spine proximally. Compound spine formula on segments seven–ten variable, may differ between left and right oviger, spine formula segments seven–ten, 2–4; 2: 1 or 2: 1; each spine bears two or three lateral denticulations. Terminal claw equal in length to segments 9 and 10 combined; 1–2 denticles may be present on inner margin, sometimes absent.

Measurements (mm) of oviger segments ♂ holotype (those of ♀ allotype in brackets). 1, 0·08 (0·04); 2, 0·09 (0·06); 3, 0·08 (0·11); 4, 0·23 (0·18); 5, 0·25 (0·20); 6, 0·11 (0·10); 7, 0·08 (0·07); 8, 0·04 (0·05); 9, 0·03 (0·03); 10, 0·04 (0·0?); claw 0·07 (0·07).

LEGS: Femur the longest segment, cement glands not evident; tibia 2 longer than tibia 1; in female coxae 1, 2 and femur dilated. Propodal heel absent, sole bearing about 12 spines. Terminal claw slender, longer than propodus. Auxiliary claws absent. Genital pores present on ventral surface of second coxae of all legs in both sexes, those of ♂ smaller than ♀.

Measurements (mm) of ♂ holotype (♀ allotype in brackets): length trunk (frontal margin of cephalon to tip 4th lateral process) 0·84 (0·80); width across 2nd lateral process 1·03 (0·87); diameter of trunk 0·16 (0·15); greatest width of cephalon 0·26 (0·30); height of ocular tubercle 0·25 (0·20); length of scape 0·36 (0·35); length of proboscis (ventral) 0·32 (0·32); length of abdomen 0·28 (0·25). Third leg: coxa 1 0·18 (0·18); coxa 2 0·28 (0·22); coxa 3 0·18 (0·15); femur 0·48 (0·45); tibia 1 0·40 (0·38); tibia 2 0·43 (0·40); tarsus 0·21 (0·20); propodus 0·32 (0·30); claw 0·34 (0·35).

DISCUSSION.

The occurrence of ovigerous males and gravid females dispels Fry's (1978 p.44) suspicion that the only other species, *Hemichela micrasterias* Stock, 1954 was based on a teratological or juvenile form. Ovigerous males carry about 70 eggs in a gelatinous mass wrapped around both ovigers. Protonymphon larvae are carried on the trunk surface of the male mainly confined to the ventro-distal surface of each lateral process. Protonymphons possess a small, distally tapering proboscis flanked by fully chelate chelifores. At the base of each chela there is a long hollow spine through which a cement gland opens. Two pairs of lateral appendages are present each terminating in a long claw bearing a single denticle on the inner margin. Okuda (1940) demonstrated in *Achelia alaskensis* (Cole, 1904) that these appendages metamorphose into palps and ovigers respectively. Eyes not evident. Coinciding with the distribution of protonymphons are 'stellate' outgrowths which I believe are the same as those referred to by Norman (1908, p. 22) and Stock (1978, p. 204) as being present on *Paranymphon spinosum* Caullery, 1876. In *H. longiunguis* these outgrowths occur on males only and appear to be composed of a cement-like material. Outgrowths appear to be related to the distribution of protonymphon.

H. longiunguis is distinguished from *H. micrasterias* by the possession of pronounced lateral processes on the second palp segment (absent in *H. micrasterias);* in the great length of the terminal claw (longer than propodus in *H.*

longiunguis, less than half as long in *H. micrasterias*); only two denticles on the dactylus (six in *H. micrasterias*) and in the oviger spine formula (*H. longiunguis* segments 7–10 with one–four compound spines, *H. micrasterias* with one or two).

The specific name, *longiunguis* (long claw) alludes to the great length of the terminal claw.

Family COLOSSENDEIDAE Hoek, 1881
Genus *Rhopalorhynchus* Wood-Mason, 1873
Rhopalorhynchus tenuissimum (Haswell, 1884)
Fig. 5 A–J

SYNONYMY:
Colossendeis tenuissima Haswell, 1884, pp. 1029–30, pl. LVI figs 5–8.
Rhopalorhynchus tenuissimus Flynn, 1919 pp. 71–2, pl. XVIII figs 1–3.
Rhopalorhynchus tenuissimum Stock, 1958, p. 125.

MATERIAL EXAMINED: Holotype: Port Denison Queensland 1 ♂ AM G5193. Other material: Calliope R., 3 ♂ 1 ♀ (grav.) 4 juv. Stns. 12/1/1 QM S910; 12/8/3, 12/1/1, 8/5/1, 21/5/5, 19/11/1, 15/4/1, 19/9/2, 15/9/5, NMV K80.

DISTRIBUTION: Only known from the Queensland coast.

DISCUSSION.
I have re-examined the holotype and confirm Flynn's (1919, p. 70) opinion that the specimen has suffered as a result of being mounted on a glass slide. The proboscis has been considerably distorted and owing to the amount of detritus adhering to the ovigers it is not possible to determine accurately the features of the distal segments. The chelate nature of the terminal oviger segment as portrayed by Haswell (1884 fig. 7) is not at all clear. An object resembling a spine similar to that figured by Haswell can be distinguished. I am uncertain as to whether this is a partly obscured spine similar to that found in the Gladstone specimens (Fig. 5 I), an imperfection in the mounting medium, or some foreign material. The legs have been mounted independently of the trunk without any indication of their correct sequence and as a result of a broken cover slip only four legs have their terminal segments intact.

Stock (1958) proposed six standard measurements with which the shape of a proboscis can be described with reasonable precision. In *Rh. tenuissimum* however, the stalk expands distally

to merge with the inflated part. Because of this it is not possible to determine accurately the junction of the two parts. The problem is especially difficult in juveniles where the basal stalk tapers for most of its length. In the absence of a clearly defined point from which the length of the inflated part may be measured, the position of the tooth when expressed as a percentage of the inflated part becomes somewhat arbitrary. The reference point from which my measurements have been taken are indicated with an arrow in Figure 5 G–H.

In the holotype the lateral processes are separated by about five times their basal diameter. A strong proboscis denticle is present at 44% of the inflated part. The basal 'stalk' is short, (36% of the total proboscis length). The sixth-seventh palp segment ratio is 82%. The tarsal ratio of the four legs is 86–98%; the tarsus is equal to, or shorter than the propodus and the terminal claw varies in length from 57–62% of the propodus.

Examination of the new material suggests that the relative lengths of the leg and trunk segment are largely age dependent. (Measurements of juveniles in brackets.) In males, lateral processes are separated by about eight times their own basal diameter (juveniles four–six times). The sixth-seventh palp segment ratio is 65–70% (65–83%). The tarsal ratio is 97–114% (118–135%). The tarsus is equal to or longer than the propodus (shorter in juveniles) and the terminal claw-propodus ratio is 69–83% (55–61%). The strong proboscis denticle is present at 44–50% of the inflated part. In the solitary female, lateral processes are separated by approximately six times their own basal diameter and the basal 'stalk' is 38% of the total proboscis length (46–48% in males). The fact that the female and juvenile forms resemble the holotype more closely than do the adults is puzzling. The presence of what appears to be a small genital pore on the ventrodistal surface of one leg in the holotype suggests that the specimen is an adult male, but in view of the above anomalies and the presence of only one pore, this may not be the case.

In view of the close geographic proximity to the type locality and the close morphological agreement, in particular the size and position of the proboscis denticle, I have assigned the present material to *Rh. tenuissimum.*

Measurements (mm) of proboscis ♂ 12/1/1, ♀ 19/11/1, NMV K80: α 3·18, 3·45 β 1·02, 1·23: γ 2·15, 3·04: δ 1·90, 1·83: ε 0·65, 0·90: ζ 0·27, 0·32.

Rh. tenuissimum falls into the closely related longitarsal group within the *kroeyeri* section (proboscis with dorsal denticle) of the genus (Stock, 1958). The other species in this group are *Rh. kroeyeri* Wood-Mason, 1873, *Rh. lomani*

Stock, 1958 and *Rh. sibogae* Stock, 1958. Of these species *Rh. lomani* is the most distinctive, having an eye tubercle with a strong apical point and a narrowly produced proboscis with the denticle distinctly before the middle of the inflated
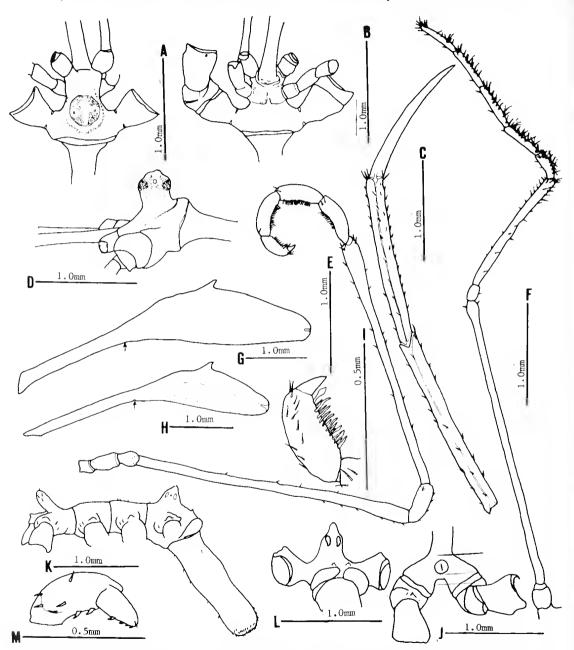
FIG. 5. *Rhopalorhynchus tenuissimum* A, Cephalic region, dorsal view, male; B, Cephalic region, ventral view, male; C, Leg 3, distal segments, male; D, Cephalic region, lateral view, male; E, Oviger, male; F, Palp, male; G, Proboscis, female; H, Proboscis, male; I, Oviger, distal segments male; J, Abdomen, ventral view, male. *Endeis straughani* K, Trunk, lateral view, female; L, Cephalic region, anterior view, female; M, Oviger, distal segments, male.

part (32–38%). *Rh. kroeyeri, Rh. tenuissimum* and *Rh. sibogae* all agree in having a low conical eye tubercle. *Rh. tenuissimum* appears closes to *Rh. sibogae* with which it agrees in the general shape of the proboscis and by possessing a strong dorsal denticle (small in *Rh. kroeyeri*). In the position of the dorsal denticle *Rh. tenuissimum* is intermediate between *Rh. sibogae* (39–43%) and *Rh. kroeyeri* (49–54%). As in *Rh. lomani,* the tarsus in *Rh. tenuissimum* may be longer or shorter than the propodus. The tarsal ratio of *Rh. sibogae* (85–99%) falls within the range of that for *Rh. tenuissimum*. The ratio of palp segment six to seven in *Rh. tenuissimum* differs from that of both *Rh. sibogae* and *Rh. kroeyeri* (50–66%).

I have not examined specimens of *Rh. kroeyeri* or *Rh. sibogae,* however on the basis of published descriptions it is difficult to find characters which are not shared by at least one of the other species suggesting that *Rh. tenuissimum* may be an intermediate form linking *Rh. kroeyeri* and *Rh. sibogae.*

ACKNOWLEDGEMENTS

LITERATURE CITED

ARNAUD, F., 1972. Pycnogonides des récifs coralliens de Madagascar. 3. Famille des Callipallenidae. *Tethys suppl.* **3**: 157–64.
1973. Pycnogonides des récifs coralliens de Madagascar. 4. Colossendeidae, Phoxichilidiidae ét Endeidae. *Tethys* **4** (4): 953–60.

BAMBER, R.N., 1979. A new species of *Endeis* (Pycnogonida) from West Africa. *Zool. J. Linn. Soc.* **65**: 251–4.
CALMAN, W.T., 1927. 28. Report on the Pycnogonida. Zoological Results of the Cambridge Expedition to the Suez Canal, 1924. *Trans. Zool. Soc. Lond.* **22** (3): 403–10.
1937. The type-specimens of *Pallene australiensis* Hoek (Pycnogonida). *Ann. Mag. Nat. Hist.* (10) **20**: 530–4.
1938. Pycnogonida. *The John Murray Expedition. Sci. Rep. 1933-34.* **5** (6): 147–66.
CARPENTER, G.H., 1892. Pycnogonida. Reports on the zoological collections made in Torres Straits by Prof. A.C. Haddon, 1888-89. *Sci. Proc. R. Dublin Soc.* **7** (5) (40): 552–8.
1907. Percy Sladen Trust Expedition to the Indian Ocean 7. Pycnogonida. *Trans. Linn. Soc. Lond.* (2) **12**: 95–101.
CHILD, C.A., 1975. Pycnogonida of Western Australia. *Smithson. Contr. Zool.* **190**: 1–28.
1963. Australian Pycnogonida. *Rec. Aust. Mus.* **26** (1): 1–81.
CLARK, W.C., 1963. Australian Pycnogonida. *Rec. Aust. Mus.,* **26**(1): 1–81.
1970. New Pycnogonida from Queensland. *Trans. Roy. Soc. NZ. (Biol. Sci.)* **12**(3): 13–20.
COLE, L.J., 1904. Pycnogonida of the West Coast of North America. *Harriman Alaska Expedition.* **10**: 249–330.
FLYNN, T.T., 1918. On a pycnogonid of the genus *Halosoma,* from New South Wales. *Pap. Proc. Roy. Soc. Tasm.* **1918**: 11–5.
1919. A re-examination of Professor Hawell's types of Australian Pycnogonida. *Pap. Proc. Roy. Soc. Tasm.* **1919**: 70–92.
FRY, W.G., 1978. A classification within the pycnogonids. In, Sea Spiders (Pycnogonida). *Zool. J. Linn. Soc. Lond.* **63** (1 + 2): 35–58.
HASWELL, W.A., 1884. Pycnogonida of the Australian coast with descriptions of new species. *Proc. Linn. Soc. N.S.W.* **9**: 1021–33.
HEDGPETH, J.W., 1948. The Pycnogonida of the western North Atlantic and the Caribbean. *Proc. U.S. Natn. Mus.* **97** (3216): 157–342.
HILTON, W.A. 1942. Pycnogonids from Hawaii. *Occ. Pap. Bernice P. Bishop Mus.* **17** (3): 43–55.
HOEK, P.C.C., 1881. Report on the Pycnogonida dedged by HMS Challenger 1873–76. *Rep. Sci. Res. Voy. Challenger* **3** (10): 1–167.
LIPKIN, Y. and U., SAFRIEL, 1971. Intertidal zonation on rocky shores at Mikhmorer (Mediterranean, Israel). *J. Ecol.* **59** (1): 1–30.

LOMAN, J.C.C., 1908. Die Pantopoden der Siboga-Expedition. *Siboga Exped. Monogr.* **40**: 1–88.

MARCUS, E. DU BOIS-REYMOND, 1959. Ein neuer Pantopode aus Foraminiferensand. *Kieler Meeresforsch.* **15** (1): 105–7.

NAKAMURA, K. 1981. Post embroyonic development of a pycogonid, *Propallene longiceps. J. Nat. Hist.* **15**: 49–62.

NORMAN, C.A. 1908. The Podosomata (= Pycnogonida) of the temperate Atlantic and Arctic Ocean. *J. Linn. Soc. Lond. (Zool.)* **30**: 198–238.

OKUDA, S., 1940. Metamorphosis of a pycnogonid parastitic in a hydromedusa. *J. Fac. Sci. Hokkaido Imperial Univ. (Zool.* 6) **7** (2): 73–86.

SAENGER, P., W. STEPHENSON, and J. MOVERLEY, 1980. The Estuarine Macrobenthos of the Calliope River and Auckland Creek, Queensland. *Mem. Qd Mus.* **20** (1): 143–61.

SCHIMKEWITSCH W., 1909b. Nochmals über die der Periodicität in dem System det Pantopoden. *Zool. Anz.* **34** (1): 1–13.

STAPLES, D.A., 1979. Three new species of *Propallene* (Pycnogonida: Callipallenidae) from Australian waters. *Trans. Roy. Soc. S. Aust.* **103** (4): 85–93.

STOCK, J.H., 1951. 5. Pantopoda. Résultats Scientifiques des Croisières de la Navire-École Belge *Mercator. Mém. Inst. r. Sci. nat. Belg.* (2) **43**: 1–2.

1954. Pycnogonida from Indo-West-Pacific, Australian and New Zealand waters. Papers from Dr Th. Mortensen's Pacific Exped. 1914–1916. *Vidensk. Meddr dansk naturh. Foren.* **116**: 1–168.
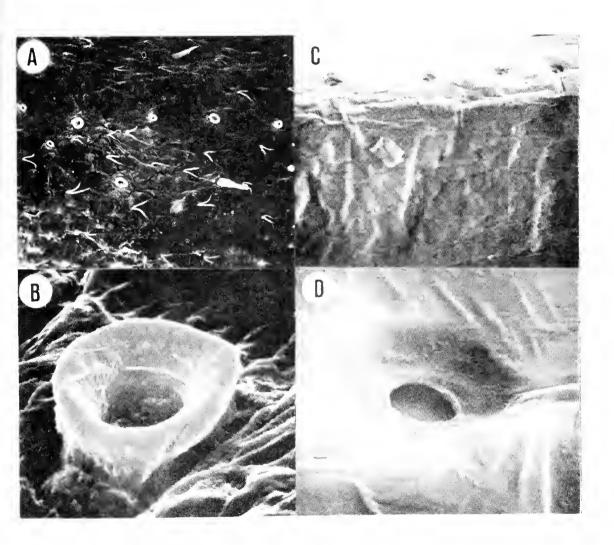
1955. Pycnogonida from the West Indies, Central America and the Pacific Coast of North America. Papers from Dr Th. Mortensen's Pacific Expedition 1914–1916.

Vidensk. Meddr dansk naturh. Foren. **117**: 209–66.

1958. The pycnogonid genus *Rhopalorhynchus* Wood-Mason, 1873. *Tijdschr. Entom.* **101** (2): 113–37.

1965. Pycnogonida from the southwest Indian Ocean. *Beaufortia* **13** (151): 13–33.

1968a. Pycnogonides. Faune marine des Pyrenees-Orientales. *Vie Milieu* **19** (1A) Suppl.: 1–38.

1968b. Pycnogonida collected by the *Galathea* and Anton Bruun in the Indian and Pacific Oceans. *Vidensk. Meddr dansk naturh. Foren.* **131**: 7–65.

1973a. Pycnogonida from south-eastern Australia. *Beaufortia* **20** (266): 99–127.

1973b. *Achelia shepherdi* n. sp. and other Pycnogonida from Australia. *Beaufortia* **21** (279): 91–7.

1975. Pycnogonida from the continental shelf, slope, and deep sea of the tropical Atlantic and East Pacific. Biological results of the University of Miami deep-sea expedition, 108. *Bull. Mar. Sci.* **24** (4): 957–1092.

1978. Abyssal Pycnogonida from the North-eastern Atlantic Basin part 1. *Cah. Biol. Mar.* **XIX**: 189–219.

1979. *Anoplodactylus ophiurophilus* n. sp. a sea spider associated with brittle stars in the Seychelles. *Bijdr. Dierk. (Contr. Zool).* **48** (2): 156–60.

WHITELEGGE, T., 1889. List of the marine and freshwater invertebrate fauna of Port Jackson and the neighbourhood *J. Proc. Roy. Soc. N.S.W.* **23**: 163–325.

WILLIAMS, G., 1941. A revision of the genus *Anoplodactylus* with a new species from Queensland. *Mem. Qd Mus.* **12**: 33–9.

WOOD-MASON, J., 1873. On *Rhopalorhynchus Kröyeri,* a new genus and species of Pycnogonida. *J. Asiat. Soc. Bengal.* **42** (2): 171–5.

PLATE 1
Endeis straughani A, Cement gland ducts (x 300); B, Cement gland duct (x 5600); *Anoplodactylus simplex* C, Cement gland ducts (x 400); D, Cement gland duct (x 2800) (S.E.M. photographs).

ON THE MYGALOMORPH SPIDER GENUS *XAMIATUS* RAVEN (DIPLURINAE : DIPLURIDAE) WITH THE DESCRIPTION OF A NEW SPECIES

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ABSTRACT

The female of *Xamiatus kia* Raven and a new species, *X. ilara,* are described. *X. ilara* is the first *Xamiatus* described from open forest.

INTRODUCTION

Xamiatus Raven, 1981 is one of Australia's largest diplurine spiders (carapace length about 14 mm, leg span about 100 mm) and is diagnosed by large feathery hairs on the coxae of leg I and of the palp. *Xamiatus* is known from the rainforests of the Evelyn Tableland (*X. magnificus*), northeast Queensland, from Bulburin State Forest (*X. bulburin*) and from the D'Aguilar, Conondale and Jimna Ranges (*X. rubrifrons*) in southeast Queensland, and from the Coff's Harbour region (*X. kia*), north coastal New South Wales (Raven, 1981). This paper adds a fifth and only (known) open forest species from the Blackdown Tableland, mid-east Queensland. Generic characters are given in Raven (1981) and not repeated here. The abbreviations AM = Australian Museum and QM = Queensland Museum; other abbreviations, methods and terminology are explained in Raven (1981). All measurements are in millimetres.

XAMIATUS KIA RAVEN
Figs. 1–4, Table 1

Xamiatus kia Raven, 1981, p. 358.
Female AM KS6999.

Carapace 14·30 long, 12·60 wide. Abdomen 16·1 long, 9·00 wide.

COLOUR IN ALCOHOL: Carapace and legs orange brown, chelicerae red-brown. Dorsal and ventral abdomen dark brown.

CARAPACE: Numerous brown bristles on posterior lateral carapace margin. Striae well defined as glabrous areas between ridges covered with lanceolate grey hairs and some black bristles. 6–8 bristles criss-cross on clypeal edge; some anteromedial bristles. Fovea strongly procurved. 1 pair of foveal bristles discernible. Clypeus about 0·19 wide.

EYES: On a low tubercle. Group is 0·22 times head-width, and 2·58 times wider than long. Front-row centres procurved; back-row centres slightly recurved. Ratio of AME:ALE:PME:PLE, 16:15:9:11. Ratio of MOQ back-width:front-width:length, 34:53:22. Eye interspaces: AME-AME, 5; AME-ALE, 4; ALE-PLE, 4; PME-PLE, 1.
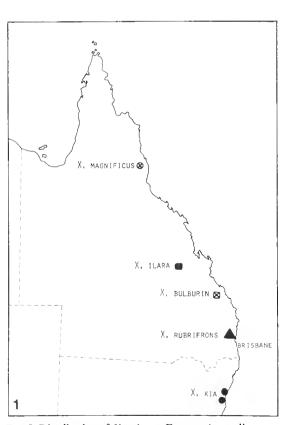
FIG. I. Distribution of *Xamiatus.* Eastern Australia.

CHELICERAE: Stout. Covered with 3 bands of brown bristles, most medial band interspersed with grey lanceolate hairs. Promargin of furrow with 15 teeth of uniform size; basomesally with 10 finer teeth. Pseudorastellum of 20 conical teeth on inner edge of chelicerae.

LABIUM: 3·35 wide, 1·81 long. Separated from sternum by two separate narrow sigilla. Cuspules absent.

MAXILLAE: 6·06 long behind, 4·39 long in front, 2·97 wide. Heel slightly incurved over labium. With about 100 cuspules confined to roughly triangular area anteriorly.

STERNUM: 7·10 long, 6·58 wide. Six sigilla, shape, length and distance from lateral margin: posterior, long oval, 1·00, 0·81; middle, long oval, 0·58, 0·65; anterior, oval, 0·35, 0·42.

LEGS: 4123. Feathery hairs on interface of posterior maxillae and coxae I, on prolateral palpal femur and prolateral femur I, and on prolateral and retrolateral palpal trochanter. Scopula on metatarsi and tarsi I, II and on papal tarsi.

SPINES: No spines on leg tarsi. *Leg 1:* femur, pl; patella, 0; tibia, p2v6; metatarsus, p2v6. *Leg 2:* femur, pl; patella, 0; tibia, p2v6; metatarsus, p2v6. *Leg 3:* femur, p3r3; patella, p2; tibia, p2r3v6; metatarsus, p4r3v10. *Leg 4:* femur, rl; patella, rl; tibia, p2r4v7; metatarsus, p5r4v12. *Palp:* femur, pl; patella, 0; tibia, v7; tarsus, v2.

CLAWS: STC of legs I and II with 4–5 teeth per row; STC of legs III and IV with 1–4 teeth per row. ITC bare, short. Palpal claw with 5 teeth in a prolateral row.
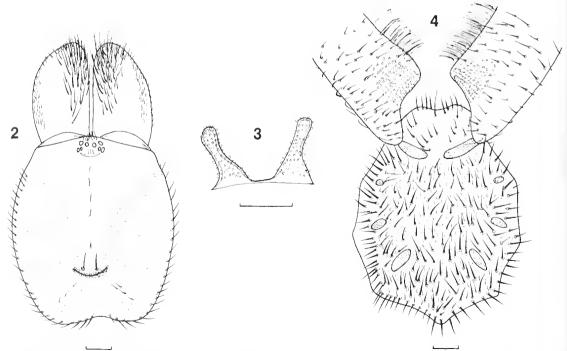
TRICHOBOTHRIA: About 10 in each row on tibiae for proximal two-thirds; an irregular row of about 25 on metatarsi; about 25 in an irregular row on tarsi. Tarsal organ distinct, raised.

SPINNERETS: PMS 1·81 long, 0·65 wide, and 1·16 apart. Basal, middle, apical, and total segments of PLS, 3·35, 2·06, 3·35, 8·76 long respectively.

SPERMATHECAE: Elongate digitiform.

TABLE 1. LEG MEASUREMENTS OF *XAMIATUS KIA*, VALUES ARE FOR FEMALE AM KS6999.

	Leg I	Leg II	Leg III	Leg IV	Palp
Femur	11·10	9·80	8·55	10·90	8·15
Patella	6·05	5·47	5·25	5·65	4·55
Tibia	8·10	7·03	5·40	8·15	5·60
Metatarsus	7·45	7·26	7·57	11·40	—
Tarsus	4·25	4·01	4·58	4·71	5·85
Total	36·95	33·57	31·35	40·81	24·15

FIGS 2-4. *Xamiatus kia*, female: 2, Cephalothorax and chelicerae; 3, Spermathecae; 4, Sternum, maxillae and labium. Scale lines = 1 mm, except Fig. 2 = 2 mm.

REMARKS:

The elongate spermathecae of *X. kia* resemble those of *X. magnificus* from north Queensland. If the elongate spermathecae are synapomorphic for those two species, then the two type-localities were continuous with each other but not with the intervening areas. I consider that possibility highly unlikely and the hypothesis of the monophyly of *X. kia* and *X. magnificus* falsified. A more parsimonious hypothesis is that the elongate spermathecae are plesiomorphic or are parallelisms.

MATERIAL EXAMINED:

The types and the following: ♀, Nambucca Heads, 30°39'S, 153°00'E, 25.xi.1957, B. Pickett, AM KS6999; ♂, near Bellinger River, 7 km from Bellingen, 30°27'S, 152°54'E, Oct. 1958, B.J. Casey, AM KS970; ♂, Bellingen, 11.xi.1933, Dr G.H. Hewitt, AM KS7001; ♂, Macksville, 30°43'S, 152°55'E, 14.xi.1978, R. Lamberth, AM KS2324; ♂, Nambucca Heads, N.S.W., 30°39'S, 153°01'E, 25.x.1977, Coll. Peterkin, AM KS971; ♂, Bowraville, 30°39'S, 152°51'E, 13.xii.1977, AM KS3465. All in New South Wales.

XAMIATUS ILARA, SP. NOV.
Figs. 1, 5–12, Table 2

TYPES:

Holotype, ♂, allotype ♀, Blackdown Tableland, Queensland, 23°48'S, 149°08'E, 2–6.ii.1981, D. Rentz, D. Wynne, G. Monteith, R. Raven, QM S741,2; 5 ♀, same data but, coll. R. Raven, QM S743.

DIAGNOSIS:

Very large spiders, carapace length about 14 mm. Males with small retrolateral distal spur and megaspine on tibia I; metatarsus I slightly excavate; palpal bulb roughly spherical with broad embolic origin; embolus wide with broad flattened scoop-shaped flange. Spermathecae of females, each a broad cup-shaped lobe, medially joined.

MALE HOLOTYPE: QM S741

Carapace 14·60 long, 12·78 wide. Total length (including chelicerae) 30·87.

COLOUR IN ALCOHOL: Carapace and chelicerae deep reddish brown, legs deep reddish brown. Abdomen grey black.

CARAPACE: Uniformly hirsute with fine black bristles and grey lanceolate hairs adpressed to surface on interstrial ridges. 2 long curved bristles between AME; several fine bristles criss-cross on clypeal edge; striae narrow, well-defined. Fovea deeply procurved in front of which is transverse groove. Thick black bristles on posterior and lateral margins.

EYES : On a distinct raised tubercle. Group is 0·27 times head-width, and 2·13 times wider than long. Front-row centres procurved; back-row centres recurved. Ratio of AME:ALE:PME:PLE, 24:19:14:20. Ratio of MOQ back-width: front-width: length, 61:46:35. Eye interspaces: AME-AME, 10; AME-ALE, 7; ALE-PLE, 7; PME-PLE, 4.

CHELICERAE: Short, stout. Covered with short lanceolate hairs and long black bristles in darker bands. Prolateral distal edge with 19 coniform teeth forming rastellum. Promargin of furrow with 12 teeth; basomesally with 8 finer teeth. Maxillary lyra absent.

LABIUM: 2·56 wide, 1·31 long.
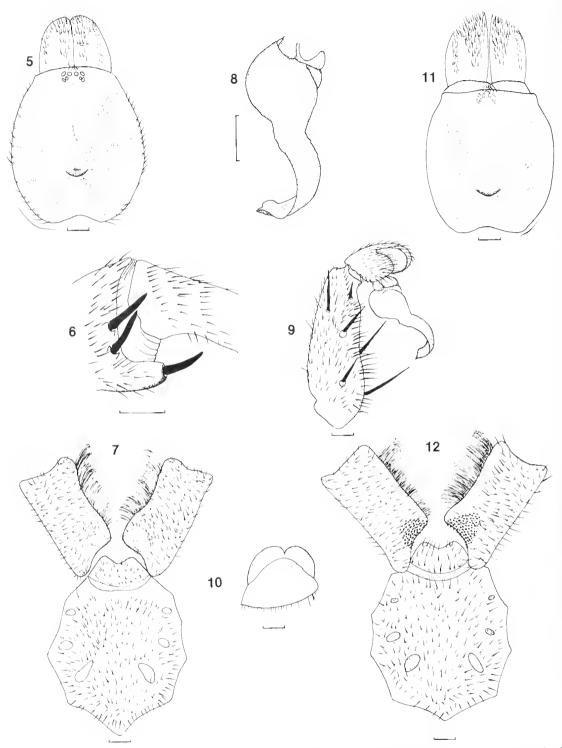
MAXILLAE: 5·31 long behind, 4·38 long in front, 2·31 wide. With about 60 cuspules in roughly quadrangular pattern in tight group on mound. Serrula absent.

STERNUM: 7·30 long, 6·40 wide. Margins concealed by inner coxae. With lanceolate hairs and long bristles. Six sigilla, shape, length and distance from lateral margin: posterior, spindle-shaped, 0·93 (0·52 wide), 0·76; middle, oval, 0·44, 0·40; anterior, sub-circular, 0·28, 0·60.

LEGS: (Table 2). 4123. Tibia I with a small retrolateral distal spur and small megaspine; metatarsus I slightly excavate. Distribution of feathery hairs: full length of prolateral palpal

TABLE 2. LEG MEASUREMENTS OF *XAMIATUS ILARA*,
VALUES ARE FOR HOLOTYPE MALE, WITH ALLOTYPE FEMALE IN PARENTHESES.

	Leg I	Leg II	Leg III	Leg IV	Palp
Femur	12·53 (10·68)	11·56 (9·58)	10·72 (8·81)	12·75 (11·00)	8·30 (7·76)
Patella	6·55 (6·10)	6·05 (5·80)	5·50 (4·84)	6·14 (5·84)	4·56 (4·35)
Tibia	9·85 (7·71)	8·42 (6·43)	7·06 (5·38)	9·65 (8·11)	6·45 (5·65)
Metatarsus	10·20 (6·48)	9·36 (6·37)	9·77 (7·85)	13·31 (10·65)	— —
Tarsus	6·75 (4·28)	5·86 (4·20)	5·70 (3·76)	5·76 (4·73)	3·30 (5·35)
Total	45·88 (35·25)	41·25 (32·38)	38·75 (30·64)	47·61 (40·33)	22·61 (23·11)

FIGS 5–12. *Xamiatus ilara*, male holotype, female allotype. 5–9, Male: 5, Cephalothorax and chelicerae; 6, prolateral tibia and metatarsus 1; 7, sternum, maxillae and labium; 8, palpal bulb; 9, prolateral tibia and tarsus, palp. 10–12, Female: 10, Spermathecae; 11, Cephalothorax and chelicerae; 12, sternum, maxillae and labium. All scale lines = 1 mm except for Figs 5, 11 = 2 mm.

trochanters; prolateral coxae, trochanters and femora I; prolateral coxae II–IV with short hairs. Upper surface of prolateral coxae I–IV with stout bristles. Scopulae on metatarsi I and II, on tarsi I–IV; scattered scopuliform hairs on metatarsi III and IV. Scopulae on all tarsi with pattern of hair colours: laterally black with orange-yellow medial band divided by two narrow bands of black hair.

PALP: No scopula on tarsi. Tarsi elongate, ventrally excavate. Bulb roughly spherical with broad embolic origin; embolus wide with broad flattened flange.

SPINES: No spines on leg tarsi. *Leg 1*: femur, p2r2; patella, p1; tibia, p3r2v6 + megaspine; metatarsus, v2. *Leg 2*: femur, p3d1r3; patella, p2; tibia, p2r1v7; metatarsus, p2v6. *Leg 3*: femur, p2d1r2; patella, p2r1; tibia, p2r3v7; metatarsus, p4r4v12. *Leg 4*: femur, p3d3r1; patella, p2r1; tibia, p2r3v7; metatarsus, p5r3v15. *Palp*: femur, p1, patella, 0; tibia, p1v6; tarsus, 0.

CLAWS: STC of all legs with 5–6 teeth per row; ITC short, bare.

TRICHOBOTHRIA: About 12 small on each row on tibiae; about 25 on metatarsi; about 16 on tarsi. Tarsal organ concealed by hair on leg I, a low elevated mound on leg IV.

SPINNERETS: PMS 1·19 long, 0·50 wide, and 0·81 apart. Basal, middle, apical and total segments of PLS, 1·88, 1·63, 2·06, 5·57 long respectively.

FEMALE ALLOTYPE QM S742

Capapace 14·00 long, 12·10 wide. Total length (including chelicerae) 37·90.

COLOUR IN ALCOHOL: Carapace orange-brown, chelicerae red brown, legs brown with paler glabrous longitudinal strips. Abdomen grey-black.

CARAPACE: With uniform covering of grey spathulate hairs Interstrial ridges and margins with black bristles. 3 long bristles curve over AME; bristles on clypeal edge; few fine anteromedial bristles. Fovea procurved with 'crease' in front.

EYES: On a distinct raised tubercle. Group is 0·21 times head-width, and is wider behind than in front; back width: front width: length, 77:70:38. Front-row centres procurved; back-row centres recurved. Ratio of AME:ALE:PME:PLE, 21:15:12:19. Ratio of MOQ back-width: front-width: length, 57:38:30. Eye interspaces: AME-AME, 9; AME-ALE, 5; ALE-PLE, 9; PME-PLE, 0.

CHELICERAE: Stout. Sparsely covered with long black bristles and lanceolate hairs in darker zones. Promargin of furrow with 11 stout and 4 small teeth; basomesally with 10 finer teeth. About 12

coniform teeth on prolateral distal edge forming rastellum.

LABIUM: 2·69 wide, 1·38 long.

MAXILLAE: 5·44 long behind, 4·31 long in front, 2·44 wide. With 80–90 cuspules on mound in broad triangular area. Lyra and serrula absent.

STERNUM: 7·20 long, 6·60 wide. Short thorn-like bristles on sternum behind maxillae and between coxae IV. Six sigilla, all oval: length and distance from margin of posterior, 0·85, 1·05; middle, 0·53, 0·50; anterior, 0·25, 0·38.

LEGS: (Table 2). 4123. All legs covered with fine adpressed hairs. All coxae with stout thorn-like bristles prolaterodorsally and on inner edges. Distribution of feathery hairs: full length of prolateral palpal femora; retrolateral palpal femur; prolateral femur; most noticeable on retrolateral palpal trochanters; prolateral coxae and trochanter I; and prolateral coxae II–IV. Thin scopula on palpal tarsi, entire and silvery black on metatarsi and tarsi I and II; no scopula on metatarsi III or IV or on tarsi IV; broadly divided on tarsi III.

SPINES: No spines on leg tarsi. *Leg 1*: femur, p2; patella, p1; tibia, p1v5; metatarsus, v5. *Leg 2*: femur, p2; patella, p1; tibia, p2v5; metatarsus, p1v5. *Leg 3*: femur, p2r3; patella, p2r1; tibia, p3r2v6; metatarsus, p4r3v11. *Leg 4*: femur, r1; patella, r1; tibia, p2r3v6; metatarsus, p4r4v12. *Palp*: femur, p1; patella, 0; tibia, p1v3; tarsus, v2.

CLAWS: STC of legs I and II with 4 teeth per row; STC of legs III and IV with 2–5 teeth per row; less on inner rows. ITC concealed by hair; short, bare. Palpal claw with 4 teeth.

TRICHOBOTHRIA: About 9 in each row on tibiae; about 18 on metatarsi; about 33 on tarsi. Tarsal organ low, domed on leg I and IV, and with aperture.

SPINNERETS: PMS 1·63 long, 0·63 wide, and 1·50 apart. Basal, middle, apical and total segments of PLS, 2·50, 1·31, 2·13, 5·94 long respectively.

SPERMATHECAE: Under unproduced lobe. Each a broad cup-shaped low lobe joined medially and discharging into a common atrium.

DISTRIBUTION AND HABITAT:

X. ilara is known only from the Blackdown Tableland, west of Rockhampton, Queensland. In that area, the spiders are found in open forest often dominated by *Casuarina*. Burrows are wide-mouthed (3–4 cm in diameter) and unbranched, extending for about 40 cms downwards along an inclined plane. Just below the mouth and at the bottom of the burrow is an

enlarged chamber about 5–7 cms long and 4–5 cms high. In the end chamber, the spider binds the prey rejactamenta into the walls. The burrows are found in loose sandy soil or compact red soil and appeared to be commoner on hillsides or on slopes. Throughout the soil in the area where the types were collected, numerous specimens of the unusual new orthopteran family Cooloolidae were found.

REMARKS:

Males of *X. ilara* most closely resemble those of *Xamiatus bulburin* Raven, 1981. However, in *X. ilara,* the palpal embolus is very broad and scoop shaped, whereas in *X. bulburin,* the embolus is narrower. The occurrence of *Xamiatus* in the Blackdown Tableland poses several biogeographic questions because otherwise *Xamiatus* is known only from rainforests in the Conondale Range,

Many Peaks Range, Evelyn Tableland in Queensland and coastal forests near Coff's Harbour, New South Wales.

LITERATURE CITED

RAVEN, R.J., 1981. A revision of the Australian genera of the mygalomorph spider subfamily Diplurinae (Dipluridae, Chelicerata). *Aust. J. Zool.* **29**: 321–63.

INOLA NOV. GEN., A WEB-BUILDING
PISAURID (ARANEAE:PISAURIDAE) FROM NORTHERN
AUSTRALIA WITH DESCRIPTIONS
OF THREE SPECIES

VALERIE TODD DAVIES
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ABSTRACT

A new genus *Inola* and three new species. *I. amicabilis, I. cracentis* and *I. subtilis* are described. All 3 species build horizontal sheet webs and possess an onychium, small eyes of similar size and a large flat colulus.

INTRODUCTION

These spiders were found in north-eastern Queensland, just outside rainforest or in rainforest where the canopy was broken and more light than usual penetrated. The only other web-building pisaurid which has been described from Australia, *Dendrolycosa icadius* (Koch, 1876) n. comb., is found in open sclerophyll forest in mid-eastern and northern Queensland. It is probably a junior synonym of *D. fusca* Doleschall, 1859 from Amboina. The type of *D. fusca* is a penultimate female, however the epigyne is recognisable under the cuticle.

All specimens have been deposited in the Queensland Museum (QM). Measurements of the cephalothorax length (CL), abdomen length (AL) and of the leg segments and eyes were made with an ocular micrometer and converted to millimetres or left as ratios. Abbreviations, AME, ALE, PME, PLE and MOQ have been used for the anterior median, anterior lateral, posterior median, posterior lateral eyes and the median ocular quadrangle.

Inola gen. nov.

Large, slender long-legged spider which spins a sticky horizontal sheet web with a funnel retreat, back to a tree trunk or rock face (Figs. 2, 20). The spider runs on the top of the web. Onychium (Fig. 17) present; short scopula on anterior metatarsi. Anterior row of eyes straight, posterior row strongly recurved, all eyes small, about same size. Clypeus narrow, less than diameter AME. Labium slightly longer than wide; sternum cordate, longer than wide. Promargin of chelicera with 3 teeth; retromargin with 3 teeth. Anterior lateral spinnerets longest and broadest; large flat colulus present (Fig. 4). Single row of trichobothria (Fig. 16) on tarsi of legs, none on palpal tarsus. Superior tarsal claws with 10–11 pectinations, inferior claw with 2 pectinations (Fig. 17). Superior lorum of pedicel composed of 4 sclerites, 2 median, 2 lateral. The posterior median sclerite with projection fitting into notch on anterior sclerite (Fig. 5). Cymbium long and slender.

The genus is most readily distinguishable from *Dendrolycosa,* the other web-building pisaurid that has been described from Australia, by the pattern of the anterior dorsal abdomen. In *Dendrolycosa* there is a marked dark stripe which terminates abruptly; in *Inola* there is a pale pattern outlining the cardiac region. *'Inola'* is an Aboriginal word meaning spider.

Inola amicabilis sp. nov.

HOLOTYPE: On sheet web, The Granites Track nr Home Rule, 35 km S. Cooktown, NE.Q., D. Joffe, V. Davies 16.xi.1974, 1 ♀, QM S860.

PARATYPES: The Granites Track nr Home Rule, NE.Q., D. Joffe, V. Davies, 16.xi.1974, 3 ♂, QM S861–863, 5 ♀, QM S864–868, 2 egg-sacs, QM S869; Intake Falls, Wallaby Ck nr Home Rule, NE.Q., D. Joffe, V. Davies, 17.xi.1974, 2 ♂, QM S870–871, 4 ♂ 5 ♀, QM S872; T. Tebble, V. Davies, 2.xi.1974 (moulted 21.xi.1974), 1 ♂, QM S873; Mt Finlay nr Bloomfield, NE.Q., V. Davies, J. Covacevich, 29.xi.1975, 1 ♀ 3 ♂, juvs., QM

S881; Summit, Mt Cook, Cooktown, NE.Q., R. Raven, V. Davies, 13.xi.1975, 2 ♀ 1 ♂, juvs, QM S882.

DESCRIPTION OF FEMALE:

CL 3·83, AL 6·83. Abdomen patterned dorsally (Fig. 1), pale venter with white mid-ventral line. Legs long 4.1.2.3. (Table 1); fourth metatarsus much longer than other metatarsi; femora and tibiae pale with darker bands, metatarsi and tarsi brown. Eyes, anterior width: posterior width: length is 60:70:47. MOQ anterior width: posterior width: length is 26:29:34. AME:ALE:PME:PLE is 10:13:11:12. Maxilla longer than wide, 1:0·43. Sternum slightly longer than wide, 1:0·90. Colulus much wider than long, 1:0·64.

♀ SPINE NOTATION: *First Leg:* femur, d3 (3rd spine small), p5r5; patella, d2p0r0; tibia, d2p2r2v5(6); metatarsus, d0p2r2v4, whorl of 5 small spines distally. *Second leg:* femur, d3p4(6)r5(6); patella, d2p0r0; tibia, d2p3(2)r2(3)v4(6); metatarsus, d0p2r2v4, whorl of 5 small spines distally. *Third leg:* femur, d3p4r5; patella, d2p0r0; tibia, d2p2r2v2; metatarsus, d0p1(2)r2v3(4), whorl of 5 small spines distally. *Fourth leg:* femur, d3p4(3)r3; patella, d2p0r0; tibia, d2p2r2v1; metatarsus, d0p2r2v5, whorl of 5 small spines distally.

EPIGYNUM (Figs. 6, 7, 8): The insemination duct enters near the base of the stalked spermatheca; the fertilization duct leaves just below this junction.

VARIATION IN LENGTH: CL 3·33–4·20; AL 4·58–6·83.

WEBS AND COCOON: The webs are usually placed one below the other in tiers against a tree trunk or rock face. The egg-sac is sub-circular, about 7 mm in diameter, loosely woven and covered in debris. It is picked up in the fangs and palps if the spider is disturbed. There were 72 eggs in one egg-sac.

TABLE 1: LEG MEASUREMENTS OF ♀ *I. AMICABILIS*

	Palp	I	II	III	IV
Femur	1·33	7·58	7·42	6·42	7·92
Patella	0·67	1·58	1·67	1·25	1·33
Tibia	1·00	7·25	6·83	5·42	6·42
Metatarsus	—	8·00	7·83	6·17	9·75
Tarsus	2·00	3·17	3·00	2·17	3·08
Total	5·00	27·58	26·75	21·43	28·50

DESCRIPTION OF MALE:

CL 3·50, AL 5·42. The male is about the same size as the female but has longer legs (I 36·00, II 34·09, III 27·00, IV 35·67). Coloration and pattern are similar to the female. Spination of the legs is very much the same except that in the male there are 4 ventral spines on the posterior tibiae.

PALP (Fig. 9, pl. 1, Figs. 18, 19): Median apophysis is large, in part sclerotized and in part membraneous. The embolus is fine and curved; it lies hidden between the membraneous part of the median apophysis and the sclerotized bar of the T-shaped conductor.

VARIATION IN LENGTH: CL 3·33–3·75, AL 4·70–5·67.

The type species *I. amicabilis* nov. is named from the 'friendly' behaviour of the sexes; the penultimate male joins the penultimate female on her web prior to their final moults.

Inola cracentis sp. nov.

HOLOTYPE: On sheet web under overhang of roadside bank, Boonjee, nr Malanda, Atherton Tableland, NE.Q., R. Raven, V. Davies, 5.iv.1978, 1 ♀, QM S874.

PARATYPES: Boonjee, nr Malanda, NE.Q., R. Raven, V. Davies, 5.iv.1978, 2 ♂, QM S875–876, ♀, juv., QM S877.

DESCRIPTION OF FEMALE:
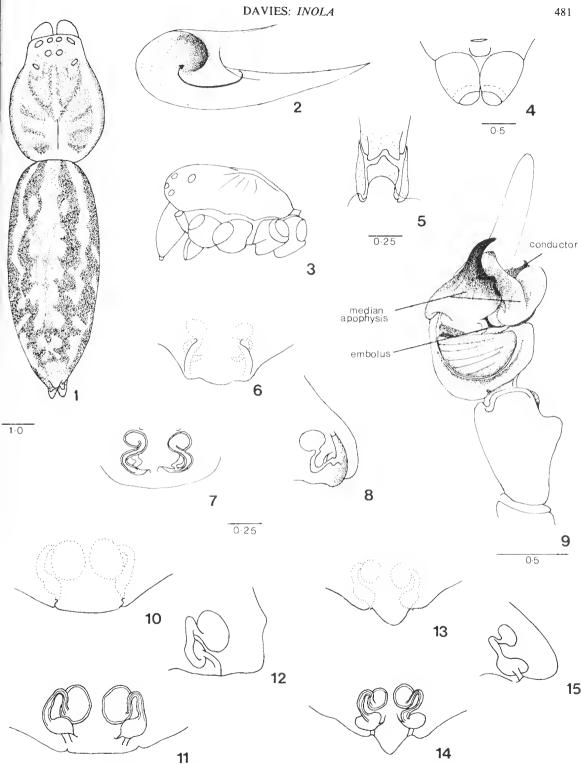
CL 4·25, AL 7·00. The spider is larger than *I. amicabilis* and has similar coloration and pattern. Legs long (I 30·41, II 29·52, III 24·50, IV 32·17). Eyes, anterior width: posterior width: length is 61:72:46. MOQ anterior width: posterior width: length is 29:32:35. AME:ALE:PME:PLE is 11:14:12:13. The disposal of spines on the legs is similar to *I. amicabilis* except that the small distal dorsal spine on femora is usually absent.

EPIGYNUM (Figs. 10, 11, 12): Spermatheca much larger than in *A. amicabilis;* insemination duct short.

VARIATION : Measurements of the paratype ♀: CL 4·58, AL 6·67.

DESCRIPTION OF MALES:

QM S876: CL 4·58, AL 6·33; QM S875: CL 4·17, AL 5·83. Colour, pattern and spination of the legs are similar to the female. Leg lengths, 4 = 1, 2, 3 (I 46·08, 40·83; II 44·42, 38·75; III 36·08; 29·92; IV 46·17, 40·75).

conductor

median
apophysis

embolus

FIGS 1–9. *Inola amicabilis.* Fig. 1, ♀, dorsal. Fig. 2, sketch of web showing columnar support and funnel retreat. Fig. 3, cephalothorax, lateral; Fig. 4, anterior lateral spinnerets, colulus. Fig. 5, superior lorum of pedicel. Figs 6–8 epigynum. Fig. 6, external. Fig. 7, internal. Fig. 8, internal, lateral. Fig. 9, ♂, palp, ventral.
FIGS 10–12. ♀ *Inola cracentis* epigynum. Fig. 10, external. Fig. 11, internal. Fig. 12, internal, lateral.
FIGS 13–15. *Inola subtilis* epigynum. Fig. 13, external. Fig. 14, internal. Fig. 15, internal, lateral.

PALP (Pl. 2, Figs. 21, 22): The sclerotised part of the median apophysis has a different shape from that of *I. amicabilis*. The embolus is more easily seen, curving upwards above the membraneous part of the median apophysis to be along the bar of the T-shaped conductor.

The specific name comes from the Latin *'cracens'* meaning graceful.

Inola subtilis sp. nov.

HOLOTYPE: On sheet web. Redlynch nr Cairns, NE.Q., R.R. Jackson, i.1980, 1 ♀, QM S878.

PARATYPES: Redlynch, NE.Q., R.R. Jackson, i.1980, 1 ♀, 1 juv., QM S879; Crystal Cascades, nr Cairns, NE.Q., R.R. Jackson, i.1980, 1 ♀, juvs. QM S880.

DESCRIPTION OF FEMALE:

CL 4·10, AL 8·30. This species is about the same size as *I. amicabilis* with similar colour and pattern. Legs long (I 28·34, II 27·42, III 22·10, IV 29·25). Eyes, anterior width: posterior width: length is 60:66:51. MOQ anterior width: posterior width: length is 27:30:32. AME:ALE:PME:PLE is 11:12:12:12. Disposal of spines on the legs is similar to *I. cracentis* with 4 ventral spines on posterior tibiae.

EPIGYNUM (Figs. 13, 14, 15): Posterior edge is extended. Insemination ducts arise at the hind edge of the epigastrium.

VARIATION: CL 4·1–4·2, AL 7·1–8·3.

The specific name comes from the Latin *'subtilis'* meaning slender.

R.R. Jackson collected the spiders while studying the behaviour of the peculiar web-invading salticid, *Portia fimbriata* (Dol.), which he found on the webs of *I. subtilis*. No males were collected.

ACKNOWLEDGEMENTS

PLATE 1
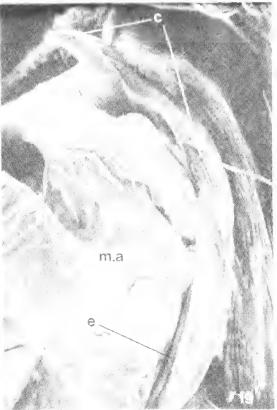
FIGS 16–17. *Inola cracentis*, S876, leg 1. Fig. 16, tarsus, trichobothrium and hairs, short scale line 10 μ. Fig. 17, tarsal claws (hairs removed), scale line 110 μ.

FIGS 18–19. *Inola amicabilis*, S875, palp. Fig. 18, prolateral, scale line 100 μ. Fig. 19, retrolateral, scale line 125 μ. c, conductor, e, embolus, m.a. median apophysis.
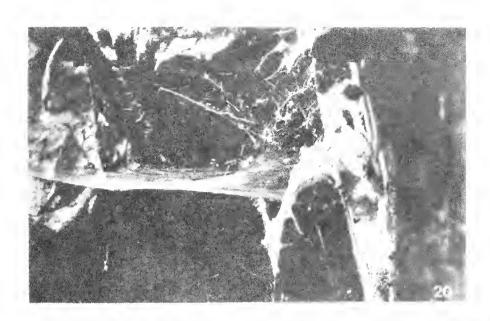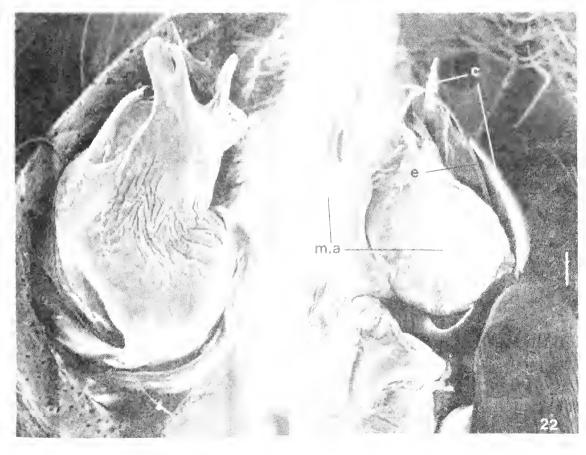
PLATE 2
FIG. 20. *Inola amicabilis* on web.
FIGS 21–22. *Inola cracentis* ♂ palp. Fig. 21, prolateral, scale line 50 μ.
   Fig. 22, retrolateral, scale line 50 μ. Abbreviations as in Fig. 19.

NEW AND LITTLE KNOWN DINOTOPERLINE STONEFLIES FROM AUSTRALIA (INSECTA: PLECOPTERA: GRIPOPTERYGIDAE)

GÜNTHER THEISCHINGER

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ABSTRACT

Two new genera, *Dundundra* and *Nescioperla,* from Queensland and a new subgenus of *Illiesoperla* McLellan, *Tonyoperla,* from New South Wales are erected. The adults of the following new species are described: *Dinotoperla arcuata* (♂, ♀), *D. cobra* (♂, ♀) and *D. leonardi* (♂, ♀) from Queensland and New South Wales, *Dinotoperla bunya* (♂, ♀), *D. cardaleae* (♂, ♀), *D. carnarvonensis* (♂, ♀), *D. duplex* (♂, ♀), *D. eungella* (♂, ♀), *D. kirrama*(♂, ♀), *D. schneiderae* (♂), *D. spinosa* (♂), *D. vulcanica* (♂, ♀), *D. wanungra* (♂), *Dundundra baiame* (♀), *Nescioperla curtisae* (♂, ♀), *Illiesoperla (I.) cerberus* (♂, ♀), *I. (I.) tropica* (♂, ♀), *Trinotoperla minima* (♂, ♀), and *T. mouldsi* (♂, ♀) from Queensland, *Dinotoperla dolichoprocta* (♂, ♀), *D. parabrevipennis* (♂, ♀), *D. pseudodolichoprocta* (♂, ♀), *Neboissoperla monteithi* (♂), *Illiesoperla (Tonyoperla) frazieri* (♂, ♀) and *Trinotoperla maior* (♂, ♀) from New South Wales and *Trinotoperla sinuosa* (♂, ♀) from Victoria.

Descriptions of the hitherto unknown males are given of *Dinotoperla fasciata* Kimmins and *Trinotoperla groomi* Perkins. Illustrations or diagnoses, or both, are presented of the adults of *Dinotoperla carpenteri* Tillyard (♂, ♀) and of the last instar nymphs of *Illiesoperla (I.) cerberus* sp.n., *I. (I.) franzeni* Perkins, *I. (I.) mayi* Perkins, *I. (I.) tropica* sp.n., *Trinotoperla groomi* Perkins, *T. minima* sp.n., *T. montana* Riek, *T. sinuosa* sp.n. and *T. yeoi* Perkins.

The names *hirsuta* McLellan, *fontana* Kimmins and *uniformis* Kimmins in *Dinotoperla*, *franzeni* Perkins, *mayi* Perkins, *perkinsi* McLellan and *tasmanica* McLellan in *Illiesoperla* and *groomi* Perkins, *minor* Kimmins and *montana* Riek in *Trinotoperla* are reinstated. *Dinotoperla arenaria* Hynes is considered as a junior synonym of *D. eucumbene* McLellan. It is stated that *Trinotoperla woodwardi* Perkins is certainly not synonymous with *T. irrorata* Tillyard.

INTRODUCTION

In two papers (Theischinger 1980, 1981) I presented mainly descriptive data for Australian Leptoperlinae and Notonemouridae from the Australian National Insect Collection (ANIC) in CSIRO, Canberra, the Australian Museum (AM) in Sydney, the University of New England (UNE) in Armidale and my own collection (GTS or GT).

In this paper these contributions to taxonomy are continued with a study of Dinotoperlinae, including in addition the rich material of the Queensland Museum (QM) and of the University of Queensland (UQ), both in Brisbane.

The delimitation of species in this paper relies on morphological characters, particularly of the male genitalia, and on the inference that constant and marked differences found between the various forms are due to their reproductive isolation.

Abbreviations for collector's names:

B.K. Cantrell	BKC	C.N. Smithers	CNS
G.B. Monteith	GBM	G. Theischinger	GT
S.R. Monteith	SRM	T. Weir	TW
L. Müller	LM	T.E. Woodward	TEW
F.A. Perkins	FAP	I.C. Yeo	ICY
E.F. Riek	EFR		

Key to Genera and Subgenera of Dinotoperlinae (Adults)

1   — Forewing with Rs simple 2
    — Forewing with Rs branched 5

2 (1) — Hindwing with M3 + 4 separate from Cul* .... *Dundundra*
    — Hindwing with M3 + 4 partially fused with Cul 3

3 (2) — Only 1 distal crossvein in each cell between Rs and Cula of forewing, wings normal .... *Nescioperla*
    — More than 1 distal crossvein in each cell between Rs and Cula of forewing, or (exceptionally) brachypterous 4

4 (3) — Male epiproct with two 'apical' spurs (as in Fig. 18); female with lateral lobe of paraprocts narrow (width at inner margin of cercus 1/3 full width of paraproct) ....
.... *Neboissoperla*
    — Male epiproct with one apical spur only (as in Figs 1–16); female with lateral lobe of paraprocts wide (width of inner margin of cercus 1/2 or more full width of paraproct) ....
....*Dinotoperla*

5 (1) — Hind margin of metabasisternum straight 6
    — Hind margin of metabasisternum with medial V-shaped cleft ....
....*Illiesoperla* 7

6 (5) — Series of crossveins between Cu2 and 1A in forewing .... *Eunotoperla*
    — Not more than one crossvein between Cu2 and 1A in forewing ....
.... *Trinotoperla*

7 (5) — No proximal crossveins between R and Rs .... *Illiesoperla* s.str.
    — Proximal crossveins between R and Rs .... *Tonyoperla*

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* This particular character of *Dundundra*, exceptional not only for Dinotoperlinae but also for Gripopterygidae, is discussed below under *Dundundra (q.v.)*.

DINOTOPERLA Tillyard

To avoid repetition in the following descriptive text the general descriptions are restricted to characteristic features. All species when fully mature seem to have black markings on the outer side of the base of meso- and meta-coxa and some dark dots or a dark line anteriorly along lateroventral edge of meso- and meta-thorax as well as heavily darkened ventral edges of all femora and darkened knees in all legs. There are, without exceptions, between 2 and 6 (generally 3–4) distal crossveins in all cells between Rs and Cula of forewing.

As it was not possible to obtain fully mature or perfectly sclerotized specimens of many species the degree of darkness and the development of wing pattern given in the descriptions may not be correct for individuals of other age groups.

DINOTOPERLA ARCUATA, sp.n. (Fig.1 A–E)

MATERIAL. Queensland: holotype ♂ and 8 paratypes (6 ♂, 2 ♀), Cunningham's Gap, 17.iii.1956, ICY; holotype in QM (T.8507), paratypes in UQ. 2 paratypes (♂), Cunningham's Gap, 3.ii.1958, collector unknown; 1 ♂, Cedar Ck, 9.xi.1954, TEW; 1 ♂, Highvale, 25.viii.1955, ICY; 1 ♂, Tamborine Mtn, 3.ix.1961, R.G. Winks; 1 ♂, Upper Cedar Ck, via Samford, 5.iv.1964, GBM; 1 ♂, Upper Brookfield, 3.iv.1967, GBM; 1 ♂, Samford, 2.ix.1967, K.C. Teoh; all in UQ. 1 ♂, Mt Mee, 9.i.1971, SRM; in ANIC. New South Wales: 1 ♂, Boonoo-Boonoo River, NNE. of Tenterfield, 7.xi.1976, GT and LM; in GT.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	6·0–7·5	8·0–9·5
♀	6·5–7·5	10·0–11·0

Body yellowish to dark brown. Wings almost hyaline; only very faint suffusion of pale greyish yellow; darker in pterostigma area and around distal crossveins of forewing.

MALE GENITALIA (A–E): Central sclerite of tergite X produced posteriorly into a straight substantial membranous cone. Epiproct long, not deep, keeled ventrally for about the second third of its length, with downcurved pointed apical and obtuse subapical spur. Paraprocts with short, wide base, otherwise rather long, evenly arched, almost parallel sided, with well rounded apex and very small subapical dorsal tooth. Cerci 9–11 segmented; basal segment very long, well arched with inner side concave, outer side convex. Basal sclerite of cercus very large and prominent on inner side.

FEMALE GENITALIA: Specimens teneral: Subgenital plate wide, very slightly bilobed. Paraprocts short. Hindmargin of tergite X rounded. Cerci 9–11 segmented.

AFFINITIES AND DIAGNOSIS: The closest ally of *Dinotoperla arcuata* sp.n. is probably *D. wanungra* sp.n. from Lamington National Park, but *D. carnarvonensis* sp.n. from Carnarvon Gorge and *D. vulcanica* sp.n. from Crater N.P. also appear related. Distinquishing characters of male *D. arcuata* are the very long, strongly arched basal segment of the cerci, the rather pointed and straight cone of tergite X, the long ventrally keeled and dorsally unarmed epiproct and the parallel sided, evenly arched paraprocts with their minute subapical tooth.

DISTRIBUTION: *D. arcuata* sp.n. is known from many localities in southeastern Queensland and from northeastern New South Wales. Other *Dinotoperla* species in the same localities are *D. bunya* sp.n., *D. carpenteri* Tillyard, *D. fasciata* Kimmins, *D. schneiderae* sp.n. and *D. uniformis* Kimmins.

DINOTOPERLA BUNYA, sp.n. (Fig. 2 A–D)

MATERIAL. Queensland: holotype ♂ (T.8508) and 1 paratype (♀) (T.8509), Bunya Mts, 10.viii.1955, TEW; in QM. 1 ♀, Bunya Mts, 26.iii.1957, EFR; in ANIC. 1 ♂, Cunningham's Gap, 3.ii.1958, collector unknown; in UQ.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	6·5–8·0	8·5–10·0
♀	8·0–10·0	10·8–11·0

Body variably brown. Wings with slight suffusion of brownish grey and darker patches around distal crossveins of forewing.

MALE GENITALIA (A–C): Central sclerite of tergite X hardly produced posteriorly. Epiproct long, narrow, basal two thirds bulging ventrally, apical third parallel sided with simple ventrally directed single spur. Paraprocts with strong short base, remainder boat-shaped, almost straight dorsally, slightly but evenly bowed ventrally. Cerci 11 segmented.

FEMALE GENITALIA (D): Subgenital plate about square, bulged with median incision at posterior margin. Paraprocts with long apical lobe.
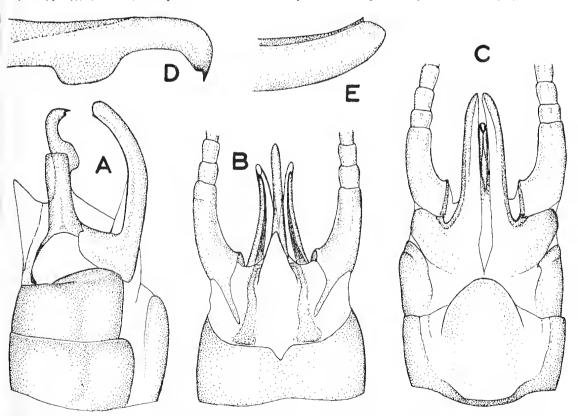
FIG. 1. *Dinotoperla arcuata* sp.n. male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, epiproct, lateral view; E: tip of paraproct, lateral view.
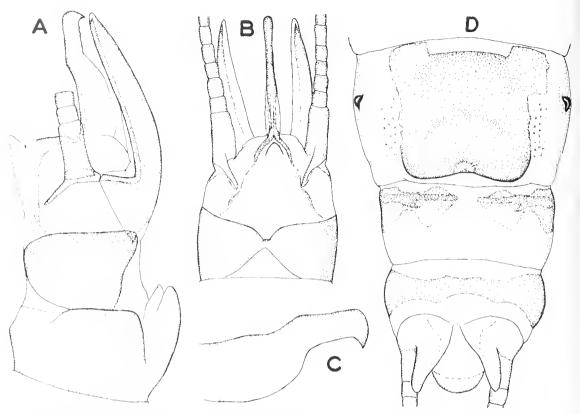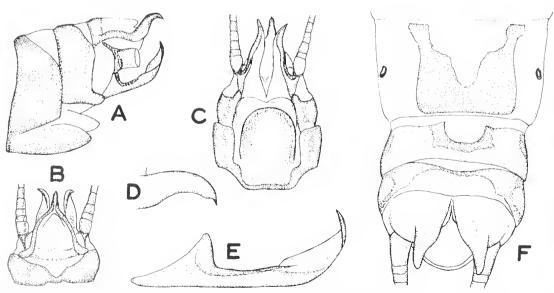
FIG. 2. *Dinotoperla bunya* sp.n.: A–C, male: A, B, genitalia: A, lateral view; B, dorsal view; C, epiproct of specimen from Cunninghams Gap, lateral view; D, female genitalia, ventral view.


3. *Dinotoperla cardaleae* sp.n.: A–E, male: A–C, genitalia: A, lateral view; b, Dorsal view; C, ventral view; D, epiproct, lateral view; E, paraproct, lateral view; F, female genitalia, ventral view.

Hindmargin of tergite X evenly rounded. Cerci with 10–11 segments.

AFFINITIES AND DIAGNOSIS: *Dinotoperla bunya* sp.n. is somewhat similar and perhaps most closely related to *D. eungella* sp.n. from Eungella Range in northern Queensland. Even from this species it can be easily separated by its simple epiproct and by its strong based almost straight and unarmed paraprocts.

DISTRIBUTION: The species is the only known *Dinotoperla* from Bunya Mountains while it coexists at least with *D. arcuata* sp.n. and perhaps with *D. schneiderae* sp.n. in Cunninghams Gap.

DINOTOPERLA CARDALEAE, sp.n. (Fig. 3 A–F)

MATERIAL. Queensland: holotype ♂ and 1 paratype (♀), Birthday Ck Falls, via Paluma, 11/12.v.1980, I.D. Naumann and J.D. Cardale; in ANIC. 10 ♀, Millaa Millaa, 9.i.1964, GBM; in UQ. Millaa Millaa Falls: 2 ♂, 4.xii.1965, GBM; 2 ♂, 13 ♀, 10/11.xii.1966, BKC; 1 ♂, 1 ♀, 12.viii.1968, TW; in UQ. 3 ♀, Mt Spec, 22.iv.1968, BKC; in UQ. Mt Spec, via Paluma: 1 ♀, 17.xii.1966, BKC; 1 ♂, 1 ♀, 21.iv.1968, GBM; in UQ. 1 ♂, 1 ♀, Mt Spec 2600ft, 4.iii.1964, I.F.B. Common and M.S. Upton; in ANIC. 3 ♀, Ringrose (= Crater) N.P., via Atherton, 9.xii.1966, BKC; in UQ. 1 ♂, Whitfield Ra., nr Cairns, 15.xii.1974, M. Moulds; in AM. 2 ♂, 3 ♀, Kirrama State Forest (Western Fall), 30.v.1971, EFR; in ANIC.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	5·5–7·0	7·5–8·5
♀	7·0–9·0	8·5–9·5

Body brownish yellow to greyish brown. Wings suffused with pale greyish yellow, brownish grey around crossveins and in pterostigma area of forewing.

MALE GENITALIA (A–E): Posteroventral corner of tergite IX produced into a rounded lobe. Central sclerite of tergite X slightly produced posteriorly into a small membranous hummock. Epiproct tapered as seen from above, an evenly curved S-shaped hook with simple pointed apical spur in lateral view. Paraprocts with moderately long and wide base, otherwise well curved dorsad, mostly slightly widened, showing an obtuse angulation dorsally, at about half length, apical part twisted inward, foliate, with pointed tip. Cerci with 10–11 segments, basal segment short.

FEMALE GENITALIA (F): Subgenital plate wide with almost straight to slightly convex posterior margin. Sclerotization on sternite IX with anteromedian semicircular excision. Paraprocts with swollen base and narrow apex. Hind margin of tergite X rounded. Cerci 10–11 segmented.

AFFINITIES AND DIAGNOSIS: *Dinotoperla cardaleae* sp.n. clearly stands out from all known congeners by its peculiar processes of tergite IX and by the twisted foliate paraprocts of the male. A closely related species is not known.

DISTRIBUTION: Being known from Kirrama State Forest, Crater N.P., Paluma, Mt Spec, Millaa Millaa and Whitfield Range the species appears to have a fairly large range. Other species of *Dinotoperla* occurring in those localities are *D. kirrama* sp.n. in Kirrama, and *D. vulcanica* sp.n. in Crater National Park.

DINOTOPERLA CARNARVONENSIS, sp.n. (Fig. 4 D–G).

MATERIAL. Queensland: holotype ♂ and 7 paratypes (3 ♂, 4 ♀), Carnarvon Gorge, 26/29.v.1954, FAP and collector unknown; holotype (T.8510), and 1 paratype (♀) (T.8511) in QM, others in UQ. 2 paratypes (♀), Carnarvon Gorge, 11/13.x.1980, GT and LM; in GT.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	7·5–8·0	9·5–11·0
♀	8·0–9·0	11·0–12·0

Body greyish yellow to blackish brown, clothed largely, but particularly between ocelli and on ventral surface of abdomen with scattered black hairs. Wings slightly suffused with brownish grey, dark patches around distal crossveins of forewing.

MALE GENITALIA (D–F): Central sclerite of tergite X only slightly produced posteriorly into a minute irregular knob-like cone. Epiproct very short and deep, narrow, very obtusely hook-like. Paraprocts with short wide and hairy base, covering part of outer side of cercus base, otherwise long, slim, evenly arched, with subapical tooth. Cerci with short basal segment and inner basal sclerite strongly developed, 13–15 segments altogether.

FEMALE GENITALIA (G): Subgenital plate wide, slightly bilobed. Posterior margin of tergite X rounded. Paraprocts short, subtriangular. Cerci 11–13 segmented.

AFFINITIES AND DIAGNOSIS: *Dinotoperla car-narvonensis* sp.n. together with *D. arcuata* sp.n., *D. vulcanica* sp.n. and perhaps *D. wanungra* sp.n. represent possibly a monophyletic group within *Dinotoperla*. *D. carnarvonensis* is distinguishable from the others by conspicuous additional scattered body hair in both sexes, and by the male having tergite X with central sclerite little developed, epiproct very short and high, cerci long and short based, and paraprocts long and large based.

DISTRIBUTION: *Dinotoperla carnarvonensis* sp.n. is the only *Dinotoperla* hitherto found at Carnarvon Gorge. It is not known from anywhere else.

DINOTOPERLA CARPENTERI Tillyard, 1921
(Fig. 5 A–F).

Tillyard (1921) described both sexes of this species from Hornsby, New South Wales.

Kimmins (1951), unable to locate the type material, repeated and tried to interpret Tillyard's description. For the same reason McLellan (1971) did not proceed any further. Hynes (1974), however, without having located the missing types, surmised the possibility that *D. carpenteri* Tillyard might be the valid name (oldest synonym) for all the forms he had united under *D. serricauda* Kimmins.

I was also unable to trace the type material but fortunately I got material matching closely

Tillyard's description and illustrations of *D. carpenteri*, from near its type locality and other places in New South Wales and Queensland. As I have no doubt that this material belongs to *D. carpenteri*, male and female genitalia are illustrated from fresh material collected in Ku-Ring-Gai Chase near Hornsby. The geographical variation shall be illustated in a future
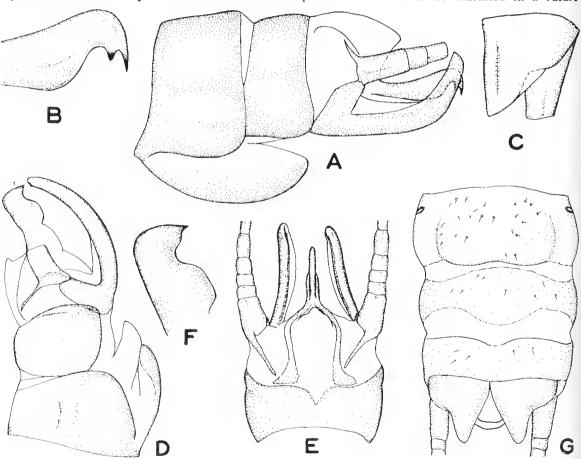
FIG. 4. *Dinotoperla duplex* sp.n.: A, B, male: A, genitalia, lateral view; B, tip of epiproct, lateral view; C, female paraproct and cercus base, ventral view. D–G, *Dinotoperla carnarvonensis* sp.n.: D–F, male: D, E, genitalia: D, lateral view; E, dorsal view; F, epiproct, lateral view; G, female genitalia, ventral view.

study (Theischinger, in preparation, on *Dinotoperla*).

MATERIAL. New South Wales: Barrington House, via Salisbury: 1 ♂, 28.v.1963, GBM; 2 ♂, 1 ♀, 18/19.xii.1963, A. MacQueen; all in UQ. 2 ♂, Barrington Tops, Allyn R. (upper), 10.x.1976, GT; 1 ♂, Blue Mts, Glenbrook, 8.x.1976, GT; 1 ♂, 1 ♀, Cangai Ck (main stream), 22.viii.1980, C.D. and G. Theischinger; 1 ♂, 3 ♀, Heathcote Brook, 10.ix.1980, GT; 1 ♂, 3 ♀, McDonald R, nr St Alban, 16.x.1976, GT; 2 ♂, Upper Falls, Royal N.P., 8.ix.1980, GT; all in GT. 4 ♂, 2 ♀, Ku-Ring-Gai Chase, 11.viii.1966, CNS; 1 ♂, Upper Allyn, 6.xi.1961, C.N. and A.S. Smithers; all in AM. Queensland: 2 ♂, Cedar Ck, Samford, 6/19.xii.1962, GBM; 1 ♂, Lamington N.P.,

4.xi.1943, collector unknown; 1 ♂, Springbrook, 11.iv.1955, R.E. Harrison; all in UQ.

AFFINITIES AND DIAGNOSIS: The affinities of *D. carpenteri* are not clear to me at all. Diagnostic features are the very long and sharply pointed paraprocts of the male and possibly the distinctively bilobed subgenital plate of the female.

DISTRIBUTION: 1 have seen what I consider to be *D. carpenteri* from several localities from Samford in southern Queensland to south of Sydney. Other *Dinotoperla* species found in these localities are *D. arcuata* sp.n., *D. cobra* sp.n., *D. dolichoprocta* sp.n., *D. fasciata* Kimmins and *D. serricauda* Kimmins.
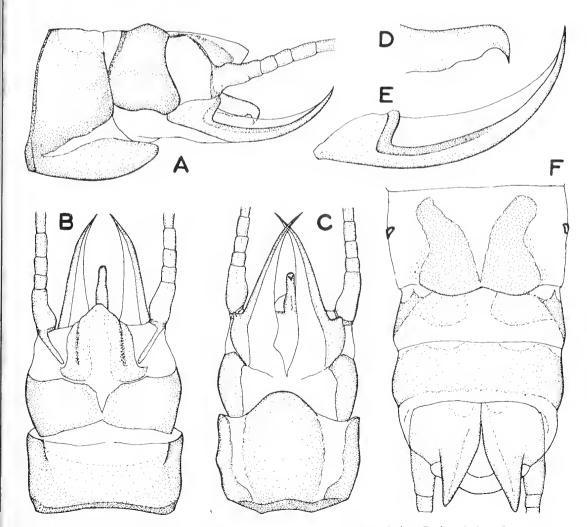

FIG. 5. *Dinotoperla carpenteri* Tillyard: A–E, male: A–C, genitalia: A, lateral view; B. dorsal view; C, ventral view; D, epiproct, lateral view; E, paraproct, lateral view; F, female genitalia, ventral view.

MEMOIRS OF THE QUEENSLAND MUSEUM

DINOTOPERLA COBRA, sp.n. (Fig. 6 A–G)

MATERIAL. New South Wales: holotype ♂ and 3 paratypes (2 ♂, 1 ♀), Barrington Tops, Upper Allyn R., 10.x.1976, GT and LM; holotype in ANIC, 3 paratypes (2 ♂, 1 ♀) in GT. 9 paratypes (5 ♂, 4 ♀), Barrington Tops, 1/5.xi.1957, FAP; in UQ. 6 paratypes (5 ♂, 1 ♀), Barrington Tops, 30.xii.1961, C.N. and A.S. Smithers; in AM. 2 paratypes (♀), Upper Allyn R., 1000–1500 ft, 8/9.xi.1960, I.F.B. Common and M.S. Upton; 4 ♂, 1 ♀, Wiangaree State Forest, via Kyogle, 18.xi.1974, SRM; in ANIC. Queensland: 1 ♂, Lamington N.P., OR, 15.xi.1955, ICY; 1 ♂, Lamington N.P., Lower Moran's 25.x.1957, ICY; 1 ♂, Upper Coomera R., 28.i.1963, GBM; 1 ♂, Lamington N.P., 22/26.xii.1967. TW; all in UQ

ADULTS: Measurements (in mm):

	Body	Forewing
♂	6·5–8·0	8·5–9·5
♀	8·0–9·0	10·5–12·0

Body variably yellowish to greyish brown. Wings with pale yellowish grey tint, darker between C and R, and greyish brown patches around distal crossveins in forewing.

MALE GENITALIA (A–E): Central sclerite of tergite X produced posteriorly into a very large pointed membranous cone. Epiproct snake-shaped (see name), long and thin, tapered as seen from above, slightly bent dorsad at about half length, with a very small tooth-like apical ventral spur. Paraprocts with very short and rather narrow base, strongly but evenly curved dorsad, with pointed tip. Cerci with 10–11 segments.

FEMALE GENITALIA (F, G): Subgenital plate very wide. Tergite X with peculiar pointed triangular median process. Cerci 11 segmented.

AFFINITIES AND DIAGNOSIS: *Dinotoperla cobra* sp.n. is possibly a close relative of *D. carpenteri* Tillyard from New South Wales and *D.*
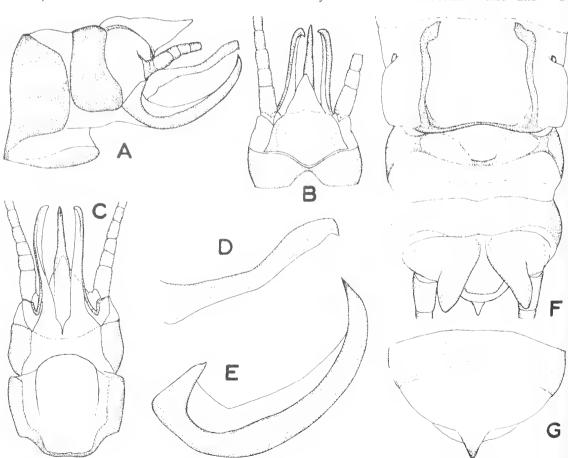
FIG. 6. *Dinotoperla cobra* sp.n.: A–E, male: A–C genitalia: A, lateral view; B, dorsal view; C, ventral view; D, epiproct, lateral view; E, paraproct, lateral view; F, G, female: F, genitalia, ventral view; G, tergite X, dorsal view.

serricauda Kimmins which ranges from Tasmania to northern New South Wales. It can be distinguished from these species and stands out from its other congeners by the extremely long and thin epiproct and its short based well curved, pointed paraprocts of the male and by the significant process on tergite X of the female.

DISTRIBUTION: The records of *Dinotoperla cobra,* sp.n., Lamington N.P. in Queensland, Wiangaree State Forest and Barrington Tops in New South Wales, suggest a fairly wide range. Species in the same localities and habitats: *D. carpenteri* Tillyard, *D. duplex* sp.n., *D. fasciata* Kimmins.

DINOTOPERLA DOLICHOPROCTA, sp.n.
(Fig. 7 A–H)

MATERIAL: New South Wales: holotype ♂ and 4 paratypes (2 ♂, 2 ♀), Brown Mtn, 18.i.1961, EFR; holotype and 2 paratypes (1 ♂, 1 ♀); in ANIC, 2 paratypes (1 ♂, 1 ♀) in GT. 1 paratype ♂, Brown Mtn, 11.xi.1961, D.H. Colless; 1 paratype ♂, Brown Mtn, 17.viii.1963, D.H. Colless; 2 ♀, Rutherford Ck, Brown Mtn, 9.viii.1962, D.H. Colless; 1 ♀, Clyde Mtn, Eastern Slopes, 26.x.1960, EFR; all in ANIC. 1 ♂, Blue Mts, Wentworth Falls, 22.xi.1960, CNS; 1 ♀, Royal N.P., 2.xii.1961, CNS; 1 ♀, Royal N.P. 27.vii.1963, D.K. McAlpine; 1 ♂, 1 ♀, Royal N.P.,
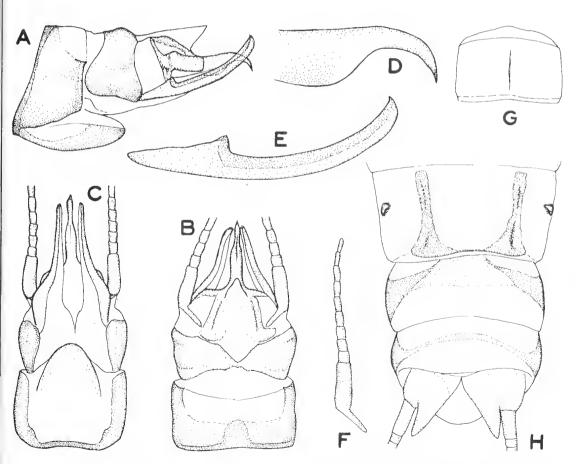

FIG. 7. *Dinotoperla dolichoprocta* sp.n.: A–F, male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, epiproct, lateral view; E, paraproct, lateral view; F, cercus. dorsal view; G, H, female: G, pronotum, dorsal view; H, genitalia, ventral view.

6.x.1965, A.S. Smithers; 1 ♂, Royal N.P., 29.xi.1968, CNS; all in AM. 3 ♂, 2 ♀, creek between Royal N.P. and Bulli, 8.ix.1980, GT; 1 ♂, 5 ♀, Minnamurra Falls, 15.x.1980, GT; 1 ♀, Bundenoon, 4.xii.1980, GT; all in GT.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	6·0–8·0	7·5–9·0
♀	8·5–10·5	8·5–10·0

Body variably yellowish to dark reddish brown. Wings slightly suffused with pale yellowish brown, markedly darker in pterostigma area and around distal crossveins in forewing.

MALE GENITALIA (A–F): Central sclerite of tergite X narrow, produced posteriorly into a well developed membranous cone. Epiproct slightly arched, a blade-shaped hook with strongly swollen base. Paraprocts with long and very narrow base, otherwise slightly curved dorsad with very small hardly upturned apical tip. Cerci slender, 9–11 segmented; basal segment long.

FEMALE GENITALIA (G–H): Subgenital plate wide, very slightly bilobed. Posterior margin of tergite X rounded. Cerci 9–11 segmented.

AFFINITIES AND DIAGNOSIS: *Dinotoperla dolichoprocta* sp.n. is very similar to *D. pseudodolichoprocta* sp.n. Diagnostic characters of *D. dolichoprocta* are a comparatively short and wide prothorax in both sexes, a narrow central sclerite of tergite X, a strong based epiproct, the narrow based paraprocts and a long basal cercus segment in male and a rounded hindmargin of tergite X in female.

DISTRIBUTION: There is material of *Dinotoperla dolichoprocta* sp.n. from Brown Mountain southeast of Canberra and from coastal New South Wales near Sydney but also from the Blue Mountains. Sympatrical *Dinotoperla* species: *D. carpenteri* Tillyard, *D. fontana* Kimmins, *D. pseudodolichoprocta* sp.n., *D. serricauda* Kimmins.

DINOTOPERLA DUPLEX, sp.n. (Fig. 4 A–C)

MATERIAL. Queensland: holotype ♂ and 5 paratypes (3 ♂, 2 ♀), Lamington N.P., O'R, 7.vii.1955, ICY, holotype (T.8512) and 1 paratype (♀) (T.8513) in QM, others in UQ. 1 ♂, labelled 2K1, and 1 ♂, 2 ♀, labelled 2A6, locality, date and collector unknown; in UQ, 2 ♂, Lamington N.P., Picnic Rk, 2/6.v.1956, ICY; 1 ♂ in UQ, 1 ♂ in GT.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	8·0–10·0	12·5–13·0
♀	8·0–10·5	14·5–15·5

Though all available specimens are young and therefore rather pale in colour they have already additional black markings on head and pronotum. Wings suffused with greyish yellow without darker patches (young specimens).

MALE GENITALIA (A,B): Central sclerite of tergite X produced only slightly posteriorly, forming a wide slightly downcurved obtuse membranous hummock. Epiproct streamlined with longer strongly downcurved pointed apical and shorter obtuse subapical spur, only a short distance between apex and ventral enlargement. Paraprocts with short wide base, otherwise strong, long, bent dorsad and slightly widened ventrally at about half length, apex not pointed. Cerci with 14–16 segments, basal segment of medium length.

FEMALE GENITALIA (C): Subgenital plate with posterior margin almost straight. Paraprocts subtriangular short and very wide. Hindmargin of tergite X rounded. Cerci 14 segmented.

AFFINITIES AND DIAGNOSIS: This large species is similar and possibly closely related to *Dinotoperla uniformis* Kimmins which ranges from at least southern New South Wales to southern Queensland. The bulky membranous hummock of tergite X, the ventrally bulging epiproct and the distinctively bent, strong paraprocts of the male and the very short and wide paraprocts of the female are specific characters of *D. duplex* sp.n.

DISTRIBUTION: The species is hitherto known from Lamington National Park only. Species found sympatric with *D. duplex* sp.n.: *D. carpenteri* Tillyard, *D. cobra* sp.n. and *D. fasciata* Kimmins.

DINOTOPERLA EUCUMBENE McLellan, 1971

As McLellan (1971) had regarded a male and a female of *Dinotoperla* with mottled wings, collected on the same day at Eucumbene River, New South Wales, as two different species — the male (*D. hirsuta*) was described as having scattered hairs on the abdomen, the female (*D. eucumbene*) not — Hynes (1974) concluded that McLellan had overlooked the abdominal hairs on that female, and regarded *D. hirsuta* McLellan a junior synonym of *D. eucumbene* McLellan by page priority. A study of the holotype of *D. eucumbene*, however, showed that it does in fact not have the scattered hairs peculiar to *D. hirsuta*,

but corresponds completely — as almost can be seen from a comparison of Figs 27A and 28A in McLellan (1971) with Fig. 14 left in Hynes (1974) — with *D. arenaria* Hynes. The two peculiarities of *D. eucumbene* as opposed to the description of *D. arenaria*, C–R crossveins and 8 cercal segments, are not unusual in a fine series of both sexes from Kiandra otherwise without any doubt matching Hynes' (1974) description of *D. arenaria*.

Thus *D. hirsuta* is not as Hynes (1974) reckoned a junior synonym of *D. eucumbene* but a quite distinct species. *D. arenaria* Hynes, however, must be regarded as conspecific with and a junior synonym of *D. eucumbene* (syn.n.). While McLellan (1971) could only give a description of a rather young female of *D. eucumbene*, Hynes (1974) described adult male and younger and older females all under *D. arenaria*.

DINOTOPERLA EUNGELLA, sp.n. (Fig. 8 A–F)

MATERIAL. Queensland: holotype ♂ and 15 paratypes (7♂, 8♀), Eungella Ra., Broken R., The Rapids, 2000ft, 27.vii.1956, TEW; holotype (T.8514) and 1 paratype (♀) (T.8515) in QM, 12 paratypes (6♂, 6♀) in UQ, 2 paratypes (1♂, 1♀) in GT. 7 paratypes (5 ♂, 2 ♀), Eungella Ra., Broken R., 17.vi.1955, A. May; 2 paratypes (♂), Eungella N.P., Broken R., 4/5.viii.1968, TW; 1 ♂, Finch Hatton Gorge, 19.iv.1968, GBM; all in UQ.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	7·0–8·0	9·5–10·5
♀	8·0–9·5	10·0–12·0

Body of the young specimens pale brownish yellow to brown with indication of usual dark markings. Wings with slight suffusion of pale brownish yellow.
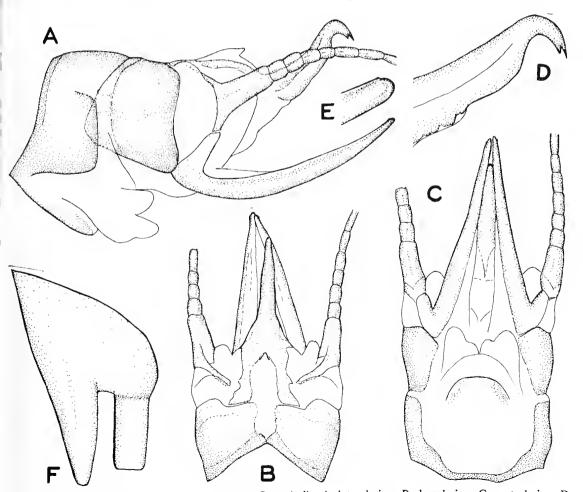

FIG. 8. *Dinotoperla eungella* sp.n.: A–E, male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, epiproct, lateral view; E, tip of paraproct, lateral view; F, female, paraproct and cercus base, ventral view.

MALE GENITALIA (A–E): Central sclerite of tergite X produced posteriorly in form of a little tip only. Epiproct tapered in dorsal view, a strong, well-rounded hook with comparatively slim end and a longer apical and a shorter subapical spur directed ventrad. Paraprocts with wide but extremely short base, otherwise very long, slim and slightly bowed dorsad, bearing a very small subterminal dorsal tooth. Cerci 10–11 segmented, basal segment long, appearing conical in lateral view.

FEMALE GENITALIA (F): All available females supposedly belonging to this species are teneral. Their subgenital plates are not at all sclerotized. The hind margin of tergite X is rounded. The apex of the paraprocts is straight and narrow and appears longer than in other *Dinotoperla* species. Cerci with 10–11 segments.

AFFINITIES AND DIAGNOSIS: *Dinotoperla eungella* sp.n. is similar to *D. bunya* sp.n. from Bunya Mountains and Cunninghams Gap. Males of *D. eungella* can be distinguished from this and all other *Dinotoperla* by their very long tergite IX, very small central sclerite of tergite X, the particular tapered epiproct and the short based, slightly arched, slender, tapered and subterminally toothed paraprocts.

DISTRIBUTION: The species is hitherto known only from the Eungella Range, where it coexists with one other *Dinotoperla* which I, having seen only a few very teneral specimens, include provisionally in *D. parabrevipennis* sp.n.

DINOTOPERLA FASCIATA Tillyard, 1924
(Fig. 9 A–E)

Only the female of this species was described by Tillyard (1924). Kimmins (1951) repeated and complemented Tillyard's description and illustrated what was left of the wings of the holotype. Hynes (1974) suspected that *D. fasciata* may be a synonym of *D. serricauda* Kimmins. The male can now be described from a large series of *D. fasciata* from many localities in Queensland and New South Wales.

MATERIAL. Queensland: Lamington N.P.: 1♀, 27.v.1955, A. Gardner; 2♂, 15.xi.1955, ICY; 1♂, Tooloona, 5.v.1956, ICY; 2♂, 23.v.1957, ICY; 1♂, 1♀, Lower Morans, 25.x.1957; 3♂, 2♀, Picnic Rk, 26.x.1957, ICY; 1♂, 1♀, Upper Coomera R., 27.v.1959, C. Cassidy; 1♀, 23.v.1962, M. Lyndon; 1♂, Upper Coomera R., 28.i.1963, GBM; 1♀, 20.v.1963, M.A. Koflick; 1♂, 10.ii.1964, GBM; 1♂, 17/21.v.1965, BKC; 1♂, 25.v.1966, TW; all in UQ. 2♂, Back Ck, near Landsborough, 10.iii.1962, K. Korboot; 1♂, Binna Burra, ?.v.1961, P. McCarrol; 2♀, Binna Burra, 22.v.1962, E. Anderson; 1♀, Highvale, 14.iv.1962, D. Taylor; 2♂, 4♀, Killarney, 2.ix.1956, ICY; 1♀, Levers Plateau, 13.iii.1966, P. McFadyen; all in UQ. New South Wales: 2♂, Pt Lookout, via Ebor, Nothofagus Forest, 4500ft, 22.i.1967, BKC; in UQ. 1♂, 1♀, Wiangaree State Forest, via Kyogle, 18.ii.1974; SRM; in ANIC.

MALE: Measurements: Body 6·5–9·0 mm; forewing 7·5–9·5 mm.
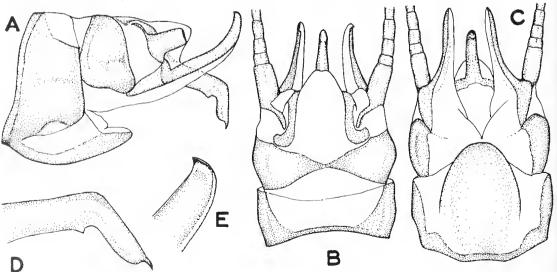
FIG. 9. *Dinotoperla fasciata* Kimmins, male: A–C, genitalia: A, lateral view, B, dorsal view; C, ventral view; D, epiproct, lateral view; E, tip of paraproct, lateral view.

Body and wings generally matching the description of the female by Tillyard (1924) and Kimmins (1951). Pronotum with well developed anterior corners. Legs darkened at knee.

GENITALIA (A–E): Central sclerite of tergite X produced posteriorly into a rather small obtuse slightly bilobed cone. Epiproct large, with apical half strongly bent ventrad and bearing an apical spur, a ventral tooth in basal half just proximal to angulation. Paraprocts with moderately long and rather narrow base, otherwise slim, with apical third bowed dorsad, tip acute and directed dorsolaterad. Cerci with 11–12 segments.

AFFINITIES AND DIAGNOSIS: *D. fasciata* is most similar to *D. christinae* McLellan. Diagnostic characters are the less pointed anterior corners of the pronotum in both sexes and the large, angulated, ventrally toothed epiproct of the male.

DISTRIBUTION: The species is known from southern Queensland and northern New South Wales. Other *Dinotoperla* species in its habitats are *D. arcuata* sp.n., *D. carpenteri* Tillyard, *D. cobra* sp.n., *D. duplex* sp.n., *D. fontana* Kimmins, *D. parabrevipennis* sp.n. and *D. uniformis* Kimmins.

DINOTOPERLA FONTANA Kimmins, 1951

Hynes (1974) synonymized *D. fontana* Kimmins with *D. serricauda* Kimmins but later (Hynes, 1976) admitted some doubt about his former concept of the variability of *D. serricauda*.

As can be seen from my discussions I regard *D. fontana* a proper species. *D. fontana* and *D. serricauda* often coexist in the same streams but — as Kimmins' descriptions and illustrations show — the male genitalia of the two species are entirely different.

DINOTOPERLA HIRSUTA McLellan, 1971

As pointed out above under *D. eucumbene* (q.v.) *D. hirsuta* cannot be regarded any longer as a junior synonym of *D. eucumbene* McLellan. *D. hirsuta* is a quite distinct species the female of which was well described by Hynes (1974) under *D. eucumbene*.

DINOTOPERLA KIRRAMA, sp.n. (Fig. 10 A–F)

MATERIAL. Holotype ♂ and 25 paratypes (19 ♂, 6 ♀), Queensland, Kirrama State Forest, via Cardwell, 17/18.viii.1966, GBM; holotype (T.8516) and 1 paratype (♀) (T.8517) in QM, 22 paratypes (18 ♂, 4 ♀) in UQ, 2 paratypes (1 ♂, 1 ♀) in GT.
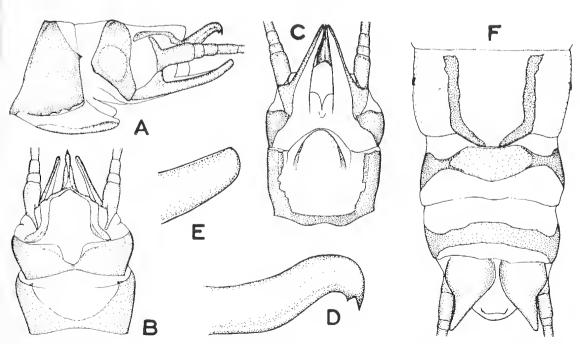
FIG. 10. *Dinotoperla kirrama* sp.n.: A–E, male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, epiproct, lateral view; E, tip of paraproct, lateral view; F, female genitalia, ventral view.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	7·0–8·0	7·0–8·2
♀	9·5–10·5	9·0–10·5

Body dark yellowish to dark reddish brown. Wings largely hyaline with tint of yellowish brown, markedly darker between C and R and along distal crossveins of forewing.

MALE GENITALIA (A–E): Central sclerite of tergite X not produced posteriorly from lateral aspect. Epiproct tapered from dorsal aspect, a rather short simple well rounded hook with a small apical and generally with a very small subapical spur, both directed ventrad. Paraprocts with moderately wide and long base, otherwise narrow, almost parallel sided, unarmed. Subgenital plate narrowly oval. Cerci with 9–10 segments.

FEMALE GENITALIA (F): Subgenital plate produced medially, hockey-stick shaped dark sclerotized area each side. Sclerotizations of sternites IX and X short, that of IX not strongly concave anteriorly. Paraprocts subconical, rather long. Tergite X rounded apically. Cerci 10–11 segmented.

AFFINITIES AND DIAGNOSIS: *Dinotoperla kirrama* sp.n. is, in my opinion, related to *D. brevipennis* Kimmins from Victoria and southern New South Wales and to *D. parabrevipennis* sp.n. from northern New South Wales. Distinguishing characters of *D. kirrama* are the tapered sides of tergite IX, the narrow subgenital plate and the simple paraprocts with their rounded tip in the male and the ventral sclerotizations of the terminal segments in the female.

DISTRIBUTION: *D. kirrama* is hitherto known only from the type locality, near Kirrama, in northern Queensland. Only one other *Dinotoperla* has ever been collected there: *D. cardaleae* sp.n.
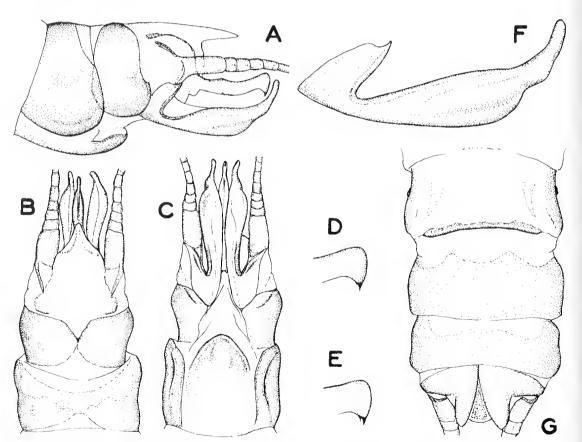
FIG. 11. *Dinotoperla leonardi* sp.n.: A–F, male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, tip of epiproct of holotype, lateral view; E, tip of epiproct of specimen from Wollondilly River, lateral view; F, paraproct, lateral view; G, female genitalia, ventral view.

DINOTOPERLA LEONARDI, sp.n. (Fig. 11 A–G)

MATERIAL. New South Wales: holotype ♂ and 1
paratype (♀), Barrington Tops, Allyn R.,
1/2.ix.1980, GT and LM; in ANIC. 1 paratype ♂,
Barrington Tops, lower Allyn R., 18.x.1976, GT
and LM; 2♂, Wollondilly R., nr Goodmans Ford,
6.x.1976, LM and GT; all in GT. Queensland: 1♂,
Killarney, 23.ix.1956, collector unknown; in UQ.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	6·0–6·5	7·0–8·5
♀	8·5	10·7

Body variably yellowish grey to dark brown.
Wings slightly suffused with pale greyish brown,
somewhat darker between C and R and dark
brownish grey patches around distal crossveins of
forewing.

MALE GENITALIA (A–F): Central sclerite of
tergite X strongly produced posteriorly from
lateral aspect. Epiproct long and slender with
ventrally directed, pointed apical spur, a small
subapical spur may be present occasionally.
Paraprocts narrowing abruptly from a short wide
base, thence widening continuously to about two
thirds length, narrowing again and bent dorsad in
two steps, tip rounded. Cerci with rather long
basal segment, 9–10 segmented.

FEMALE GENITALIA (G): In the single available
young specimen which is probably conspecific
with the holotype only the sclerotized apical
margin of a remarkably wide subgenital plate
seems to be of diagnostic value. Cerci with 11
segments.

AFFINITIES AND DIAGNOSIS: *Dinotoperla leonardi*
sp.n. is most similar and probably closest related
to *D. fontana* Kimmins. The male of *D. leonardi*
can be distinguished from *D. fontana* and other
Dinotoperla by its long, slender epiproct which is
not markedly widened dorsally and by the long
sinuous, double bent, round-tipped paraprocts.

DISTRIBUTION: The species is fairly widespread,
its known range extending from the Wollondilly
River (New South Wales) in the south to
Killarney (southern Queensland) in the north.
Dinotoperla species found sympatrical with *D.
leonardi* sp.n. are: *D. fasciata* Kimmins, *D.
fontana* Kimmins, *D. serricauda* Kimmins and *D.
uniformis* Kimmins.

DINOTOPERLA PARABREVIPENNIS, sp.n.
(Fig. 12 A–F)

MATERIAL. New South Wales: holotype ♂ and 5
paratypes (2 ♂, 3 ♀), New England N.P.,
21.ii.1966, EFR; holotype and 3 paratypes (1 ♂, 2
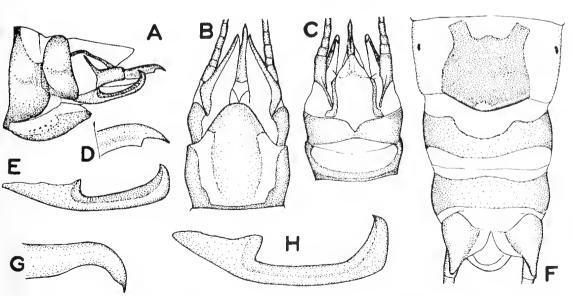
FIG. 12. A–F, *Dinotoperla parabrevipennis* sp.n.: A–E male: A–C, genitalia: A, lateral view; B, ventral view; C,
dorsal view; D, tip of epiproct, lateral view; E, paraproct, lateral view; F, female genitalia, ventral view. G, H,
Dinotoperla parabrevipennis sp.n., male, from Eungella Range: G, epiproct, lateral view; H, paraproct, lateral
view.

♀), in ANIC, 2 paratypes (1 ♂, 1 ♀) in GT. 5 paratypes (1 ♂, 4 ♀), New England N.P., Pt Lookout, 21.iv.1960 and 3 paratypes (2 ♂, 1 ♀), same locality, 16.i.1964, C.W. Frazier; all in UNE. 9 paratypes (4 ♂, 5 ♀), New England N.P. 4.i.1966, CNS; 1 ♂, 3 ♀, Barrington Tops, Gummi Falls, Rain Forest, 30.xii.1961, C.N. and A.S. Smithers; all in AM.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	6·0–7·5	6·5–8·5
♀	7·5–9·0	8·0–9·0

Body yellowish to dark brown. Wings faintly suffused with yellowish grey, conspicuous brown patches around distal crossveins of forewing.

MALE GENITALIA (A–E): Central sclerite of tergite X produced posteriorly into a substantial cone. Epiproct narrow, slightly but evenly arched ventrad for its whole length, with pointed apical spur, directed posteriorly rather than ventrally, and obtuse subapical tooth some distance from apex. Paraprocts with moderately long and wide base, otherwise short, rather widening towards the end, slightly arched dorsad, with pointed apex, curved to the anterior. Cerci with 8–9 segments.

FEMALE GENITALIA (F): Subgenital plate broadly darkened and sclerotized, produced medially but not angulated. Sclerotizations of sternite IX and X moderately long, that of IX with semicircular median excision anteriorly. Paraprocts conical, short. Cerci 8–9 segmented. Tergite X with rounded tip.

AFFINITIES AND DIAGNOSIS: *Dinotoperla parabrevipennis* sp.n. is considered closely related to *D. brevipennis* Kimmins from Victoria and southern New South Wales and to *D. kirrama* sp.n. from northern Queensland. *D. parabrevipennis* is distinguishable from its allies by the conical central sclerite of tergite X, the very slightly arched epiproct with obtuse distantly subapical tooth and the upturned pointed end of the paraprocts in male. The female stands out by a convex posterior margin of the subgenital plate and the semicircular median excision of the sclerotization of sternite IX.

DISTRIBUTION: The species is known from New England Range and from BarringtonTops, both in northern New South Wales. Some material from Eungella Ra. (4 very young ♂, Broken R., 4/5.viii.1968, T. Weir; in UQ) is provisionally placed here (Fig.12 G,H). *D. cobra* sp.n. has been found sympatrical with *D. parabrevipennis*.

DINOTOPERLA PSEUDODOLICHOPROCTA, sp.n. (Fig.13 A–G)

MATERIAL. New South Wales: holotype ♂ and 5 paratypes (4 ♂, 1 ♀), Blue Mountains, Wentworth Falls, 11.ix.1980, GT; holotype and 1 paratype (♀) in ANIC, 4 paratypes (♂) in GT. 3 paratypes (♂), Blue Mountains, 22.xi.1960, D.K. McAlpine; 1 paratype (♂), Blue Mountains, Wentworth Falls, 22.xi.1960, CNS; all in AM. 1 paratype (♀), Blue Mountains, Wentworth Falls, 15.xi.1980, GT; in GT.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	6·0–7·5	6·5–7·5
♀	6·5–8·0	6·5–7·5

Body yellowish to blackish brown, wings faintly suffused with greyish brown; dark greyish brown patches around distal crossveins of forewing.

MALE GENITALIA (A–D): Central sclerite of tergite X wide, produced posteriorly into a small membranous cone. Epiproct simple, slightly arched, blade-shaped. Paraprocts with moderately long and wide base, otherwise slightly curved dorsad, tip upturned. Cerci 13–16 segmented, basal segment very short.

FEMALE GENITALIA (F–G): Subgenital plate bilobed. Posterior margin of tergite X angulated. Cerci 12–15 segmented.

AFFINITES AND DIAGNOSIS: *Dinotoperla pseudodolichoprocta* sp.n. is most similar and probably closest related to *D. dolichoprocta* sp.n. The specific characters of *D. pseudodolichoprocta* are a rather long and narrow prothorax in both sexes, the basally wide central sclerite of tergite X and the many segmented, short based cerci in the male and the bilobed subgenital plate and the angulated hind margin of tergite X in the female.

DISTRIBUTION: *Dinotoperla pseudodolichoprocta* sp.n. is known only from the Blue Mountains in New South Wales, where it exists sympatrically with *D. carpenteri* Tillyard, *D. dolichoprocta* sp.n., *D. fontana* Kimmins and *D. serricauda* Kimmins.

DINOTOPERLA SCHNEIDERAE sp.n. (Fig. 14 A–E)

MATERIAL. Queensland: holotype ♂ and 1 paratype (♂), Mt Mee, ?.i.1971, SRM; holotype in QM (T.8518), paratype in UQ. ?1♂, Cunningham's Gap, 17.iii.1956, ICY; in UQ.

MALE: Measurements: Body 7·5–8·0 mm; forewing 8·0–8·5 mm.

Body variably yellowish to dark brown. Wings with slight suffusion of pale brown, markedly darker in pterostigma area, along distal part of longitudinal veins and surrounding crossveins of forewing.

GENITALIA (A–E): Central sclerite of tergite X slightly sclerotized basally, produced posteriorly into a huge, more or less pointed membranous cone. Epiproct a large strongly bent hook with long pointed apical and short obtuse subapical spur, both directed ventrally, a few dorsal spines in basal half. Paraprocts with long base, otherwise rather short, bowed dorsad, sinuously widened dorsally in apical third, with pointed tip. Cerci 11–12 segmented.

AFFINITIES AND DIAGNOSIS: *Dinotoperla schneiderae* sp.n. is considered closely related only to *D. spinosa* sp.n. from Mt Tozer in northern Queensland. Its diagnostic characters are the spiny epiproct and the slender, subterminally widened, pointed paraprocts.

DISTRIBUTION: The species is hitherto known with certainty only from Mt Mee in southeastern Queensland, the record from Cunningham's Gap remains somewhat doubtful. On Mt Mee it was found sympatric with *D. arcuata* sp.n., at Cunningham's Gap the two other species were *D. arcuata* sp.n. and *D. bunya* sp.n.

DINOTOPERLA SPINOSA, sp.n. (Fig. 14 F, G)

MATERIAL. Holotype ♂, Queensland, Iron Ra., Mt Tozer, 300 m, 30.iv.1973, SRM; in ANIC.

MALE: Measurements: Body 5·0 mm; forewings with distal portion missing. Body and wings of the unique male (very young) pale greyish yellow.

GENTALIA (F, G): Central sclerite of tergite X a huge pointed membranous cone. Epiproct a large hook with apical part slightly arched, very thin and narrow; a long pointed apical and a shorter subapical spur; base with several dorsal spines. Paraprocts strong, distinctively excavated on outer
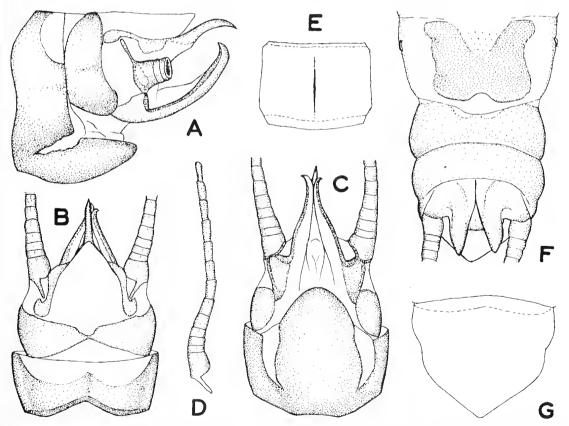
FIG. 13. *Dinotoperla pseudodolichoprocta* sp.n.: A–D, male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, cercus, dorsal view; E–G, female: E, pronotum, dorsal view; F, genitalia, ventral view; G, tergite X, dorsal view.
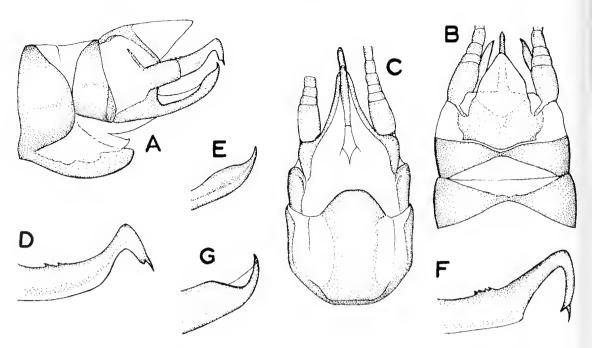
FIG. 14. A–E, *Dinotoperla schneiderae* sp.n., male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, epiproct, lateral view; E, tip of paraproct, lateral view. F, G, *Dinotoperla spinosa* sp.n., male: F, epiproct, lateral view; G, tip of paraproct, lateral view.
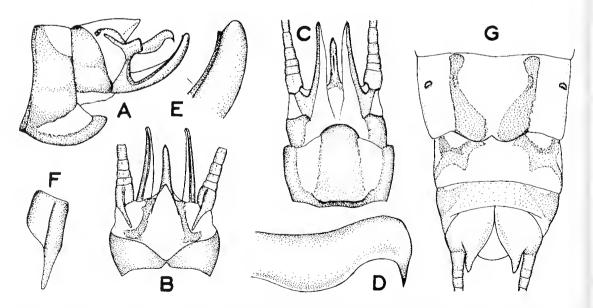
FIG. 15. *Dinotoperla vulcanica* sp.n.: A–F, male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, epiproct, lateral view; E, tip of paraproct, lateral view; F, basal cercus segment, dorsal view; G, female genitalia, ventral view.

side adjacent to strongly upturned tip. Cerci with 13 segments.

AFFINITIES AND DIAGNOSIS: *Dinotoperla spinosa* sp.n. is considered closely related to *D. schneiderae* sp.n. from Queensland. Diagnostic characters of *D. spinosa* are the unusual prolongation of the apical part of the epiproct and the laterally excavated paraprocts.

DISTRIBUTION: The species is known at the present only from the type locality (Mt Tozer). No other *Dinotoperla* have been reported there.

DINOTOPERLA UNIFORMIS Kimmins, 1951

Hynes (1974) considered *D. uniformis* Kimmins a junior synonym of *D. serricauda* Kimmins but later (Hynes, 1976) expressed some doubt about his former concept of the variability of *D. serricauda*. As my discussions show I regard *D. uniformis* a proper species. *D. uniformis* often coexists with *D. serricauda* and as Kimmins' (1951) descriptions and illustrations clearly demonstrate the male genitalia of the two species are strikingly different.

DINOTOPERLA VULCANICA, sp.n. (Fig. 15 A–G)

MATERIAL. Queensland: holotype ♂ and 2 paratypes (1 ♂, 1 ♀), The Crater, Atherton Tableland, 25.iv.1970, S.R. Curtis; holotype and 1 paratype (♀) in ANIC, 1 paratype (♂) in GT. 2 paratypes (♂), The Crater, nr Herberton, 18.xii.1974, M.S. Moulds; in AM.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	6·0–7·0	7·0–8·5
♀	9·2	9·5

Body yellowish to dark brown. Wings suffused with pale yellowish brown, considerably darkened between C and R, particularly in pterostigma area and around all crossveins of forewing.

MALE GENITALIA (A–F): Central sclerite of tergite X produced posteriorly into a substantial membranous cone. Epiproct simple, slightly S-curved with birdshead-shaped apex. Paraprocts with short wide base, otherwise slightly arched dorsad and very slightly narrowing towards apex which is well rounded and armed with a very small subapical dorsal tooth. Cerci with very short longitudinally strengthened basal segment, 9–10 segmented.

FEMALE GENITALIA (G): Subgenital plate produced onto sternite IX, narrow, bilobed. Sclerotization on sternite IX interrupted medially. Paraprocts with narrow and rather pointed apex. Posterior margin of tergite X rounded. Cerci 10 segmented.

AFFINITIES AND DIAGNOSIS: *Dinotoperla vulcanica* sp.n. is probably related to *D. arcuata* sp.n. from southeastern Queensland and north eastern New South Wales, *D. wanungra* sp.n. from Lamington N.P., and to *D. carnarvonensis* sp.n. from Carnarvon Range. Diagnostic characters of male *D. vulcanica* are short paraprocts with simple base, a long sinuous epiproct, a rather short first cercus segment and a basal cercus sclerite of normal shape (not overdeveloped as in the three species mentioned).

DISTRIBUTION: *Dinotoperla vulcanica* sp.n. appears to be an endemic *Dinotoperla* of Crater National Park in Atherton Tableland; it coexists there with *D. cardaleae* sp.n.

DINOTOPERLA WANUNGRA, sp.n. (Fig. 16 A–E)

MATERIAL. Holotype ♂, Queensland, Lamington National Park, Mt Wanungra, 15.vi.1963, GBM; in QM (T.8519).

MALE: Measurements: Body 10·0 mm, forewing 9·5 mm.
Body in the single available and discoloured specimen yellowish grey. Wings without distinctive pattern.

GENITALIA (A–E): Central sclerite of tergite X produced posteriorly into a long substantial membranous cone. Epiproct long, spearhead-shaped as seen from above, keeled ventrally, for the second third of its length, with downcurved pointed apical and obtuse subapical spur and a distinctive M-shaped dorsal tooth about one third length from base. Paraprocts with very wide and short base, otherwise long and straight, with apical quarter strongly bent dorsally and apex enlarged with small apical spine-shaped process directed to the anterior. Cerci with long, well developed basal segment, 16-segmented.

AFFINITIES AND DIAGNOSIS: The long basal cercus segment and the overall shape of paraprocts and epiproct suggest that *D. wanungra* sp.n. is closely allied to *D. arcuata* sp.n. Apart from much greater longitudinal dimensions of all genital structures the markedly upturned and enlarged tips of the paraprocts and the dorsal tooth on the epiproct clearly separate *D. wanungra* from this species.
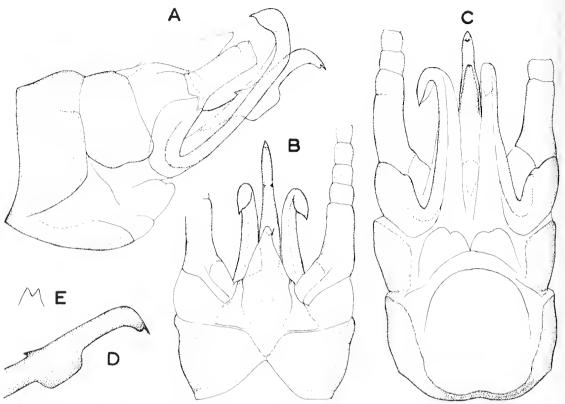
FIG. 16. *Dinotoperla wanungra* sp.n., male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, epiproct, lateral view; E, basal tooth of epiproct, dorsal view.
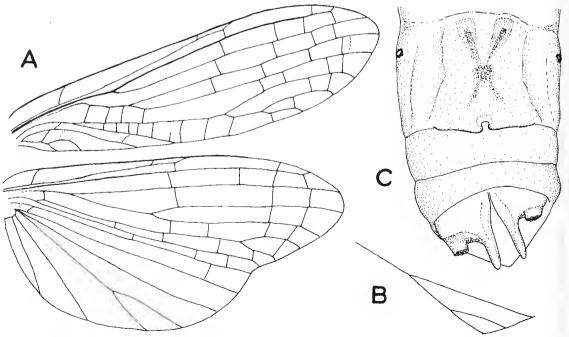

FIG. 17. *Dundundra baiame* sp.n., female: A, wings; B, triple branched 4A; C, genitalia, ventral view.

DISTRIBUTION: The species has hitherto only been collected on Mt Wanungra in Lamington National Park. Several other *Dinotoperla* species are known from the same National Park: *D. carpenteri* Tillyard, *D. cobra* sp.n., *D. duplex* sp.n., *D. fasciata* Tillyard.

DUNDUNDRA, gen.n.

TYPE SPECIES: *Dundundra baiame,* sp.n., by monotypy.

CHARACTERS: Wings unusually broad, with well visible but somewhat variable pattern. Forewing with Rs simple, M forked and Cu1 triple branched. Hindwing with Rs simple, M forked, but M3+4 never fused with Cu1; Cu1 forked; 4A forked or triple branched; 6A free of wing margin.

FEMALE GENITALIA: Subgenital plate not produced; with small deep and almost circular narrow median notch. Paraprocts with very narrow apex. Hind margin of tergite X angulated. Cerci with 14–16 segments.

AFFINITIES AND DIAGNOSIS: In wing venation (M3+4 never fused with Cu1 in hindwing) and structure of female subgenital plate (with narrow median notch) *Dundundra* clearly stands out from all known Dinotoperlinae and even Gripopterygidae. The question if *Dundundra* is a sister group of a single genus (perhaps *Dinotoperla*) a group of closely related genera (perhaps *Dinotoperla, Neboissoperla* and *Nescioperla*) or of the higher taxa mentioned above cannot be answered before the male of *Dundundra* is discovered.

DUNDUNDRA BAIAME, sp.n. (FIG. 17A–C)

MATERIAL. Queensland: Holotype ♀ and 1 paratype (♀), Lamington N.P., 30.v.1929, FAP, and 3 paratypes (♀), same locality, 30.v.1935, collector unknown but probably also Perkins; holotype in QM (T.8520), 3 paratypes in UQ, 1 paratype in GT.

FEMALE: Measurements: Body 10·0–11·5 mm; forewing 11·0–12·5 mm.

Body rather stout, variably light greyish to dark reddish brown. Antennae markedly longer than forewing. Legs long and strong, darkened for a longer distance in femora, for a shorter distance in tibiae at knees.

Wings (A, B) described under "Characters" of *Dundundra*; 3–8 crossveins in all cells between Rs and Cula; membrane greyish white with conspicuous greyish brown patches on distal crossveins in forewing, tinted largely with greyish brown all over in hindwing.

GENITALIA (C) described under "Characters" of *Dundundra*.

AFFINITIES AND DIAGNOSIS discussed under *Dundundra*.

DISTRIBUTION: Hitherto known from the type locality, Lamington N.P., only.

NEBOISSOPERLA MONTEITHI, sp.n. (FIG. 18 A–F)

MATERIAL. Holotype ♂, New South Wales, Williams R., Rocky Crossing, via Salisbury, 27.v.1963, GBM; in QM (T.8521).

MALE: Measurements: Body 7·5 mm; forewing 9·0 mm.

Body including legs in the single available young and discoloured specimen pale yellowish brown without any conspicuous markings. Wings almost hyaline; 2–4 distal crossveins in all spaces between Rs and Cula of forewing.

GENITALIA (A–F): Central sclerite of tergite X produced posteriorly into a thumb-shaped membranous lobe. Epiproct with anterior spur curved posteriorly and posterior spur curved ventrally. Paraprocts evenly bulged ventrally and slightly concave dorsally, with laterally strongly developed base and rectangular subapical dorsal tooth directed to the anterior. Cerci with the three basal segments enlarged, 17 segmented.

AFFINITIES AND DIAGNOSIS: *Neboissoperla monteithi* sp.n. is similar and closely related to the other known *Neboissoperla, alpina* McLellan, from some mountainous areas of Victoria and south eastern New South Wales. While the epiproct of these two species is almost identical in shape, the paraprocts are much less bulged ventrally and less sclerotized, with a tooth pointing in the opposite direction (to the anterior), the basal cercus segment is not at all long or curved and the next cercal segments lack dorsal projections in *N. monteithi*. By the inclusion of this new species *Neboissoperla* McLellan is taken closer to *Dinotoperla* Tillyard than when considered monotypic.

NESCIOPERLA, gen.n.

TYPE SPECIES: *Nescioperla curtisae,* sp.n., by monotypy.

CHARACTERS: Wings without pattern; forewing with Rs simple, Cu1 forked, only 1 distal crossvein in each cell between Rs and Cula; cubitoanal space with indication of 1 basal crossvein; hindwing with Rs simple, M3+4 and Cu1 separating before wing margin; generally 1 crossvein between Cu1 and Cu2.

MALE GENITALIA: Central sclerite of tergite X produced posteriorly into a very long, narrow, apically rounded and largely membranous process. Epiproct very large, a strongly angulated hook-like structure with one dorsal spur directed anteriorly and two apical spurs directed ventrad, the posterior spur being shorter than the anterior. Paraprocts very strongly developed, with long wide base, thence very narrow but widening continuously again to form a sub-apical ventral corner and a dorsad directed pointed apex. Cerci with 14 segments. A significant rounded ear-shaped, strongly sclerotized plate is situated at the inner side of each cercus base.

FEMALE GENITALIA: Subgenital plate with hind margin slightly emarginate medially. Paraprocts short, appearing wider than long in ventral view, obtuse. Hindmargin of tergite X rounded. Cerci 12–13 segmented.

AFFINITIES AND DIAGNOSIS: As indicated by the wing venation Nescioperla gen.n. is certainly most closely related to Dinotoperla Tillyard and Neboissoperla McLellan. It has however, less distal cross-veins in forewing than is known from any species of these genera. The male genitalia do not match those of either Dinotoperla or Neboissoperla or any other genera. At the present we do not know of any Dinotoperla or Neboissoperla with an anteriorly directed dorsal spur and two ventrally directed terminal spurs on the epiproct of which the posterior is the shorter one. The ear-shaped structure between cercus base and epiproct is unique. The shape of the central sclerite of tergite X in male and the female genitalia of Nescioperla appear more similar to
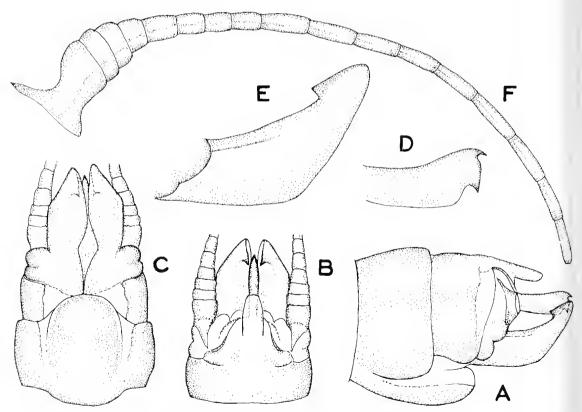
FIG. 18. Neboissoperla monteithi sp.n., male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, epiproct, lateral view; E, paraproct, lateral view, F, cercus, lateral view.

these structures of *Neboissoperla* than to those of *Dinotoperla*, while the paraprocts of the male match perhaps closer those of *Dinotoperla*.

On the reasons of these similarities a sister group relationship between *Nescioperla* and *Dinotoperla* — *Neboissoperla* could be taken into consideration.

NESCIOPERLA CURTISAE, sp.n. (Fig.19 A–F)

MATERIAL. Holotype ♂ and 1 paratype (♀), Queensland, Bloomfield R., 7/9.v.1970, S.R. Curtis; in ANIC.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	7·0	7·2
♀	8·0	8·0

Body brownish yellow to pale greyish brown with dark brown to black markings as follows: at base of all coxae, along anterolateral and ventrolateral edge of meso- and meta-thorax, along ventral edge of all femora; only slightly darkened at base of all tibiae. Wings with yellowish brown venation and very slightly pale brownish yellow suffused membrane without any pattern.

MALE GENITALIA (A–E) AND FEMALE GENITALIA (F) described under 'Characters' of *Nescioperla*.

AFFINITIES AND DIAGNOSIS discussed under *Nescioperla*.

DISTRIBUTION: *Nescioperla curtisae* is known only from the type locality, Bloomfield R., on Cape York Peninsula.
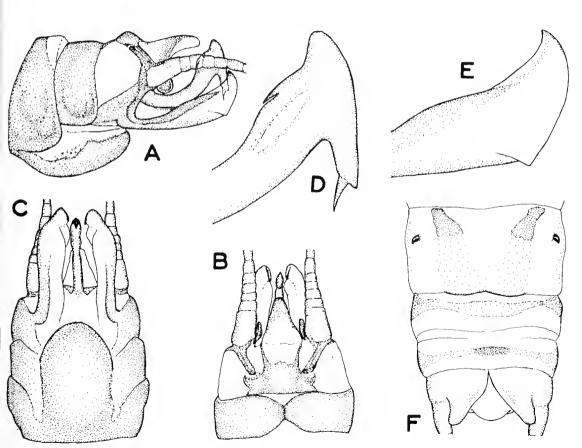
FIG. 19. *Nescioperla curtisae* sp.n.: A–E, male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, tip of epiproct, lateral view; E, tip of paraproct, lateral view; F, female genitalia, ventral view.

ILLIESOPERLA AUSTRALIS (Tillyard, 1924)

Hynes (1974) synonymized *I. franzeni* (Perkins), *I. mayi* (Perkins), *I. perkinsi* McLellan and *I. tasmanica* McLellan with *I. australis*. There are, however, marked and clear morphological differences not only in the venation and in the shape of the epiproct but also in the form of the male paraprocts which indicate distinctness of *I. franzeni*, *I. mayi*, *I. perkinsi* and *I. tasmanica* from *I. australis* on specific level.

I. australis stands out within *Illiesoperla* by the presence of pterostigma crossveins in both sexes and by a high and narrow epiproct without any dorsal tooth and rather long slender slightly arched paraprocts with their sclerotization distinctively enlarged for a short distance near cercus base in male.

MATERIAL. New South Wales: 2 ♂, 22 ♀, Bolairo, 1961–74, EFR; 14 ♂, 11 ♀, Canberra, 1935–61, EFR; in ANIC. 2 ♂, 5 ♀, Wollondilly R., nr Goodmans Ford, 6.x.1976, LM and GT and 4 ♂, 3 ♀, same locality; 20/21.ix.1980, GT; in GT.

ILLIESOPERLA CERBERUS, sp.n. (Fig. 20A–H)

MATERIAL. Queensland: holotype ♂ and 1 paratype (♀), 40 km w. of Tully, 31.x.1971, EFR; 1 ♀, Kirrama State Forest (Western Fall), 30.v.1971, EFR; 1 ♂, Little Crystal Ck, Mt Spec, 29.v.1971, EFR; 5 ♀, Moses Ck, 4 km N. by E. Mt Finnigan, 15° 47' S/145° 17' E, 14/16.x.1980, J.C. Cardale; 1 ♂, Mossman Gorge, 16.vi.1971, EFR; 5 ♀, 2 km on Mt Edith Rd, Tinaroo Dam, 23.vi.1971, EFR; 1 ♀, Mulgrave River, date and collector unknown; all in ANIC. 1 ♂, The Crater nr Herberton, 18.xii.1974, M.S. Moulds; 1 ♂, 3 ♀, Whitfield Range, nr Cairns, 24.viii.1974, M.S. Moulds; all in AM. 1 ♂, 13 ♀, Mena Ck, nr Mt Utchee, 145° 52'/17° 40', 26/27.xi.1976, LM and GT; 3 ♀, Mossman Gorge, 145° 23'/26° 27', 19/25.xi.1976, LM and GT; all in GT. 1 ♂, Bloomfield R, 3.x.1974, GBM; 1 ♂, 15 nymphs, Mossman Gorge N.P., 10.viii.1968, TW; 1 ♀, Paluma Dam, 24.xii.1963, GMB; 2 ♂, 1 ♀, Upper Mulgrave R., 30.vi.1970, GBM; all in UQ. Palmerston N.P.: 5 ♀, 29.xii.1964, GBM; 2 ♂,
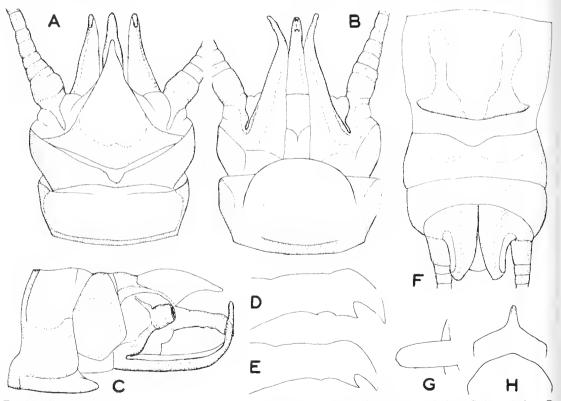
FIG. 20. *Illiesoperla cerberus* sp.n.: A–E, male: A–C, genitalia: A, dorsal view; B, ventral view; C, lateral view; D, E, epiproct, lateral view: D, from locus typicus; E, from Whitefield Range; F, female genitalia, ventral view; G, H, fully grown nymph: G, posterolateral corner of prosternum, ventral view; H, posterior margin of tergite X: top, male; bottom, female.

22.iv.1968, BKC; Henrietta Ck, 3 ♀, 5.xii.1965, GBM, and 2 ♂, 8.viii.1968, TW; via Innisfail, 1 ♀, 23.iv.1968, GBM; all in UQ.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	9·5–11·5	10·5–13·0
♀	12·5–14·5	12·0–14·0

Body largely greyish yellow to greyish brown, lighter mainly on ventral side of entire body and on inner side of femora; yellow pattern on head and on outer side of femora; two conspicuous black dots at base of meso- and meta-coxa, one black mark anteriorly on lateroventral edge of both meso- and meta-thorax. Prosternum with long, thin sausage-shaped posterolateral process. Wings, suffused faintly with brownish grey, darker along crossveins of forewing; conspicuous greyish brown patches around pterostigma crossveins in both wings.

MALE GENITALIA (A–E): Tergite X produced into a huge pointed curved membranous cone. Epiproct long, slender, almost straight, with two large somewhat backward directed pointed ventral teeth, one apical and one subapical. Papaprocts long, tapering, somewhat variably strongly curving dorsad to narrow but rounded apices. Subgenital plate wide, almost perfectly semicircular. Cerci with 11–15 segments.

FEMALE GENITALIA (F): Subgenital plate wide, somewhat produced medially, sclerotized and darkened laterally. Paraprocts slightly curved laterad, with rounded apices. Tergite X produced medially, but apex rounded. Cerci 12–14 segmented.

NYMPHS (G, H): 8·0–10·0 mm long (last instar); body greyish yellow to greyish brown with lighter pattern on head, femora and abdominal tergites. Prosternum produced strongly posterolaterally behind coxa to form sausage-shaped process. Posterior margin of tergite X as illustrated.

AFFINITIES AND DIAGNOSIS: *Illiesoperla cerberus* sp.n. appears to be a close ally of the much larger *I. australis* (Tillyard). Only these two species have really curved paraprocts and a narrow rounded incision on their bases. Both sexes of *I. cerberus* have a long, sausage-shaped process behind the procoxa and always several crossveins in the pterostigma area. Male *I. cerberus* have more pointed and backward directed ventral teeth on the epiproct and much longer, slenderer and stronger curved paraprocts than any other *Illiesoperla* species.

DISTRIBUTION: *Illiesoperla cerberus* sp.n. is known from many localities of tropical Queensland and may coexist with *I. tropica* sp.n.

ILLIESOPERLA FRANZENI (Perkins, 1958)
(Fig. 21H)

I. franzeni is not — as proposed by Hynes (1974 — regarded as a synonym of *I. australis* (Tillyard). *I. franzeni* and *I. australis* were found to coexist in the Wollondilly River in New South Wales. *I. franzeni* is easily distinguished from *I. australis* as well as from its other congeners by the lack of pterostigma crossveins in both sexes and by the very high and narrow, dorsally toothed epiproct and by pointed, dorsally sinuously curved paraprocts.

MATERIAL. New South Wales: 1 ♂, Boonoo-Boonoo R., NNE. of Tenterfield, 7.xi.1976, GT; 4 ♂, 3 ♀, Cangai Creek (main stream), 22.viii.1980, GT; 1 ♂, Wollondilly R., nr Goodmans Ford, 6.x.1976, GT, and 4 ♂, 3 ♀, same locality, 20/21.ix.1980, GT; all in GT. Queensland: as listed by Perkins (1958) on p. 96. 9 nymphs, Upper Brookfield, 28.ix.1954, colls J. Peaberdy and Y. Beri; in UQ.

NYMPHS (H): 11·0–12·0 mm long (last instar); dorsally yellowish to pale greyish brown, ventrally pale brownish yellow; no pattern discernible. Posterior margin of tergite X with narrow and very deep median process in male and with small conspicuously upturned median process in female nymph (as illustrated).

ILLIESOPERLA MAYI (Perkins, 1958) (Fig. 21I)

I. mayi is not — as proposed by Hynes (1974) — regarded as a synonym of *I. australis* (Tillyard). It can be separated from this species by its simple pointed paraprocts without enlargement of sclerotization near cercus base.

MATERIAL. New South Wales: 1 ♂, New England N.P., via Ebor, 22/23.i.1966, BKC; 1 ♂, New England N.P., 3/6.xii.1967, TW; both in UQ. Queensland: as listed by Perkins (1958) on p. 95. 8 nymphs, Lamington N.P., date and collector unknown; in UQ.

NYMPHS: 11·0–12·5 mm long (last instar); dorsally yellowish brown, ventrally pale greyish yellow, greyish brown pattern on head, pronotum and on femora. Posterior margin of tergite X about triangularly produced in male, rounded in female nymph (as illustrated).

ILLIESOPERLA PERKINSI McLellan, 1971

I. perkinsi is not regarded, as proposed by Hynes (1974), as a synonym of *I. australis* (Tillyard). It can be separated from this species by the rather low tapering epiproct and almost straight slender paraprocts without enlargement near cercus base and with upturned pointed tip.

I am, however, not yet convinced that *I. perkinsi* and *I. mayi* (Perkins) are distinct on specific level. As an attempt to resolve this problem shall be made in an extensive study of *Illiesoperla* (Theischinger, in preparation, on *Illiesoperla*) I do not list here the material I hitherto studied.

ILLIESOPERLA TASMANICA McLellan, 1971

I. tasmanica does not come close to *I. australis* (Tillyard) of which Hynes (1974) regarded it a synonym. It is however related and probably a sister species of *I. franzeni* Perkins. *I. tasmanica* has not as *I. franzeni* a distinctive basal tooth on the dorsal edge of the epiproct but only a few hardly discernible crenulations instead. It has a much larger sclerotized area on the outer side of the paraprocts than *I. franzeni* and — unusual in the genus *Illiesoperla* — many very strong dark bristles on the membraneous inner side of the paraprocts.

MATERIAL. Holotype ♂, Tasmania, creek near Burnie, 25.xi.1966, J. Illies; in ANIC.

ILLIESOPERLA TROPICA, sp.n. (Fig. 21 A–G)

MATERIAL. Queensland: holotype ♂ and 16 paratypes (5 ♂, 11 ♀) and 15 nymphs, Lockerbie Area, Cape York, 13/17.iv.1973, SRM; holotype and 14 paratypes (4 ♂, 10 ♀) in ANIC, 2
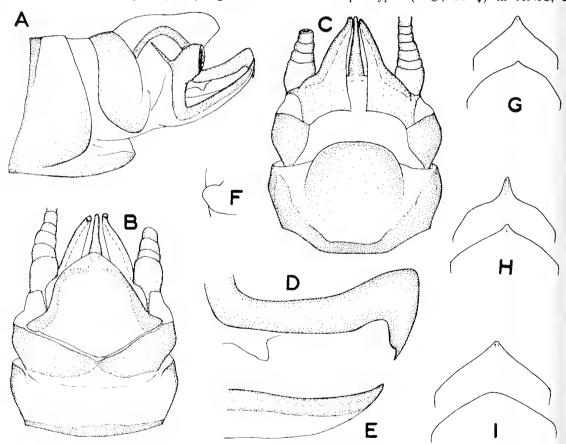
FIG. 21. A–G, *Illiesoperla tropica* sp.n.: A–E, male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, epiproct, lateral view; E, tip of paraproct, lateral view; F, G, fully grown nymph: F, posterolateral corner of prosternum, ventral view; G, posterior margin of tergite X: top, male; bottom, female. H, *Illiesoperla franzeni* Perkins, fully grown nymph, posterior margin of tergite X: top, male; bottom, female. I, *Illiesoperla mayi* Perkins, fully grown nymph, posterior margin of tergite X: top, male; bottom, female.

paratypes (1 ♂, 1 ♀) in GT. 1 ♂, 1 ♀, Iron Range, 2/9.vi.1971, EFR; 1 ♀, Iron Range, Mt Tozer Foothills, 4.vi.1971, EFR; 1 ♂, 13 nymphs, Captain Billy Ck, Cape York Pen., 142°50'E/11°40'S, 9/13.vii.1975, SRM; 1 ♂, Peach Creek Crossing, 25 km NNE of Coen, 4/5.vii.1976, G.B. and S.R. Monteith; all in ANIC. 1 ♀, 5 mi. N. Bloomfield R., 7/9.v.1970, S.R. Curtis; 3 ♂, 1 ♀, Lockerbie Scrub, Cape York, 10/15.iv.1975, M.S. Moulds; all in AM. 1 ♀, 400 yds from Mulgrave R. at Gordonvale, 23.iv.1960, B.E. Hitchcock; 2 ♂, Gap Ck, 5 mi. N. Bloomfield R., 100 ft, 8/9.v.1970, GBM; all in UQ.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	9·0–10·5	10·0–12·0
♀	10·0–12·0	10·0–12·0

Body largely yellowish to brownish grey, ventral surface pale greyish yellow, dark yellow pattern on head. Black dots at base of meso- and meta-coxa; one black patch anteriorly on lateroventral edge of both meso- and meta-thorax. Wings suffused faintly with yellowish brown, greyish brown along crossveins of forewing. No pterostigma crossveins in both wings.

MALE GENITALIA (A–E): Tergite X produced into a slightly curved huge swollen obtuse membranous cone. Epiproct long, slender, apex strongly bent ventrad and produced into a hook with a moderately long pointed apical and a shorter blunt subapical tooth. Paraprocts short, almost straight with pointed and only very slightly upturned apex; no enlargement of sclerotization near cercus base. Subgenital plate wide, about semi-circular. Cerci with 13–15 segments.

FEMALE GENITALIA: Subgenital plate wide, posterior margin convex. Posterior margin of tergite X angulated, slightly additionally produced medially. Cerci with 13–15 segments.

NYMPHS (F,G): 8·0–9·0 mm long (last instar): dorsal surface greyish brown with yellow mark between ocelli and narrow yellow midline from pronotum to abdominal tergite IX (inclusively), ventrally brownish yellow. Prosternum produced slightly posterolaterally behind coxa to form rounded knob. Posterior margin of tergite X as illustrated.

AFFINITIES AND DIAGNOSIS: *Illiesoperla tropica* sp.n. appears closest related to the much larger *I. mayi* (Perkins) from more southern regions of Queensland which it approaches in the shape of male epiproct and paraprocts as well as in the shape of the female genitalia which are very uniform throughout the genus. There are, however, several crossveins present in the pterostigma area in both wings of all *I. mayi* specimens I have seen while such crossveins are absent in all studied *I. tropica*. *I. franzeni* (Perkins) from Queensland and New South Wales lacks crossveins in the pterostigma area as does *I. tropica*, but male epiproct and paraprocts of these two forms are remarkably different.

DISTRIBUTION: *Illiesoperla tropica* sp.n. is known from several places in tropical Queensland and may coexist with *I. cerberus* sp.n.

TONYOPERLA, subgen.n.

TYPE SPECIES: *Illiesoperla (Tonyoperla) frazieri*, sp.n., by monotypy.

CHARACTERS: Wings as in *Illiesoperla* s.str. and in addition 2–5 very conspicuous proximal crossveins between R and Rs.

MALE GENITALIA: As in *Illiesoperla* s.str. but (even in aged and heavily sclerotized specimens) sclerotization of paraproct base not extending mediad (= narrow based).

FEMALE GENITALIA: As in *Illiesoperla* s.str.

AFFINITIES AND DIAGNOSIS: In the structure of male genitalia *Illiesoperla (Illiesoperla) australis* (Tillyard) comes closest to *Tonyoperla* subgen.n. Both sexes of *Tonyoperla* can be distinguished, however, from all species of *Illiesoperla* s.str. by the presence of conspicuous proximal crossveins between R and Rs in forewing, and the male by the narrow based sclerotization of the paraprocts.
NAME: named for my friend Prof. A. (Tony) F. O'Farrell, Armidale.

ILLIESOPERLA (TONYOPERLA) FRAZIERI, sp.n.
(Fig. 22 A–E)

MATERIAL. New South Wales: Holotype ♂, New England N.P., via Ebor, 22/23.i.1966, BKC; in QM (T.8522). 1 paratype ♂, New England N.P., 22.ii.1967, and 1 paratype ♂, same locality, 3/6.xii.1967, TW; both in UQ. 1 paratype ♂, New England N.P., Pt Lookout, 21.iv.1960, C.W. Frazier; in GT. 1 paratype ♂, New England N.P., nr entrance, 8.iv.1961, C.W. Frazier; 1 ♀, locality, date and collector unknown; both in UNE.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	13·5–15·0	19·0–20·0
♀	18·0	20·5

Body largely yellowish to medium brown, the light areas being particularly the ventral surface of head and thorax, the sides of meso- and meta-thorax and inner side of legs; a diamond-shaped yellow patch between ocelli, two pale yellow patches on outer side of all femora; black along posterior side of median ocellus and along proximal side of lateral ocelli, two black dots at base of meso- and meta-coxa and one brownish black to black spot anteriorly on lateroventral edge of both, meso- and meta-thorax. Wings (A) slightly suffused with greyish yellow, greyish brown some distance between C and R, markedly darker patches around all crossveins particularly in pterostigma area of forewing; hindwing with faintly darker patches around pterostigma crossveins only.
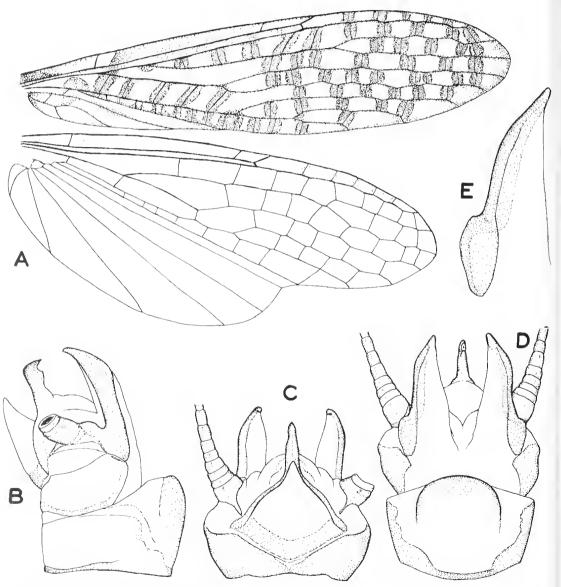
FIG. 22. *Illiesoperla (Tonyoperla) frazieri* sp.n., male: A, wings; B–D, genitalia: B, lateral view; C, dorsal view; D, ventral view; E, paraproct, ventral view.

MALE GENITALIA (B-E): Tergite X produced into a large pointed almost straight membranous cone. Epiproct rather short deep with well defined apical and not well defined subapical tooth. Paraprocts very strong; base sinuously thickened near cercus base; otherwise broad, sclerotization slightly widened at about two thirds length, tip not markedly pointed. Subgenital plate wide, well rounded. Cerci with 16–19 segments.

FEMALE GENITALIA: Subgenital plate wide, posterior margin almost straight. Paraprocts rather long. Cerci with basal segment at least as long as following 3 segments; 16 segmented. Posterior margin of tergite X produced medially into a small but distinctive tongue-shaped process.

AFFINITIES AND DIAGNOSIS: discussed under *Tonyoperla*.

DISTRIBUTION: Hitherto known only from New England N.P. where it coexists at least with *I. (I.) mayi* Perkins in the same streams.

TRINOTOPERLA GROOMI Perkins, 1958
(Fig. 23 A–F)

Hynes (1974) synonymized *T. groomi* and *T. minor* Kimmins with *T. nivata* Kimmins.

Having studied all available material of *T. groomi* I found that it certainly is a distinct species which coexists with *T. minor* for example at Lamington National Park and at Crystal
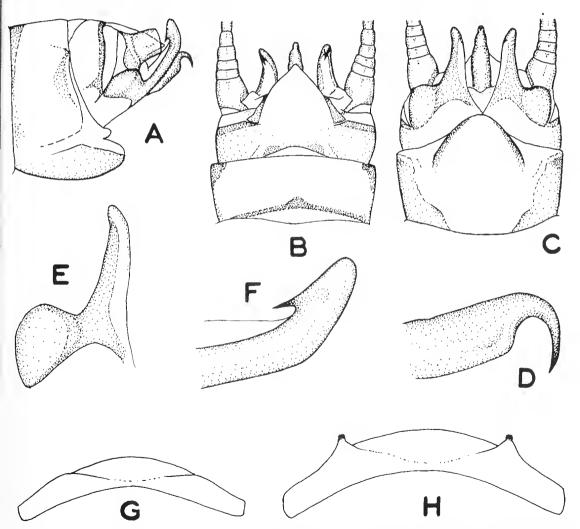

FIG. 23. A–F, *Trinotoperla groomi* Perkins, male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, epiproct, lateral view; E, paraproct, ventral view; F, tip of paraproct, lateral view. G, *Trinotoperla montana* Riek, nymphal pronotum, frontal view. H, *Trinotoperla yeoi* Perkins, nymphal pronotum, frontal view.

Cascades in Queensland. I regard *T. nivata* which has never been taken in northern New South Wales or in Queensland as a member of another species group. Perkins (1958) had unfortunately designed a male from Natural Arch, Numinbah (Queensland), which I identified in the course of this study as *T. minor,* as allotype of *T. groomi* and most probably used for the illustration of this species (Fig. 1b,c). This could be a reason why Hynes (1974) regarded *T. groomi* a synonym of *T. nivata* (and most probably *T. minor*) without seeing any *T. groomi.* Most material from Lamington National Park and the specimen from Killarney Perkins (1958) listed under *T. groomi* also belong to *T. minor.*

To prove my statements above I describe and illustrate here in detail the male of *T. groomi* from the type locality (Bunya Mountains).

MATERIAL. Queensland: Bunya Mts: Holotype ♀ and 33 paratypes (♀), 30.ix.1954, J.L. Groom and A.W. May; holotype in QM, paratypes in UQ. 2 ♀, 30.ix.1954, A.W. May; 2 ♀, 30.ix.1954, collector unknown; 4 ♀, 30.ix.1954, J.L. Groom; 1 ♀, N.P., via Toowoomba, 15.ix.1954, J.L. Groom; 1 ♀, 10 nymphs 10.viii.1955, TEW; 1 ♀, M'Grory Falls, 24.x.1958, S. Sekhon; 1 ♂, 2 ♀, 11/12.ii.1967, BKC; 1 ♀, 5.vi.1969, ICY; all in UQ; 1 ♀, 4.vii.1971, EFR; in ANIC. Crystal Cascades: 1 ♂, 2 ♀, ?.v.1963, K. Korboot; 1 ♂, ?.v.1969, K.K.; all in UQ. Eungella Ra.: 1 ♀, 19.v.1937, FAP; 1 paratype ♂, Broken R., 17.vi.1955, A. May; 2 ♂, 3 ♀, Broken R., The Rapids, 2000ft, 27.vii.1956, TEW; all in UQ; 2 ♀, Broken R., 27.v.1971, EFR; in ANIC. 1 paratype ♂, Highvale, 30.iii.1955, coll. Harrison; in UQ. Kondalilla N.P.: 1 ♀, 2.iii.1962; 1 ♂, 17.iii.1962, M.A. Tesch; in UQ. 1 ♀, Lamington N.P., 26.iii.1961, K. Legessnek; in UQ. 1 ♂, Mapleton, 12.iv.1952, J.G. Morris; in UQ. Mt Nebo: 2 ♀, 17.iv.1955, W. Horne; 1 paratype ♀, 14.vii.1955, W.R. Horne; 1 paratype ♂, 15.viii.1955, D.J. Woodland; all in UQ. 1 ♂, locality, date and collector unknown; in GT.

MALE: Measurements: Body 12·0–14·0 mm; forewing 14·0–17·0 mm. Body and wings generally matching the description of the female by Perkins (1958).

GENITALIA (A–F): Tergite X produced into a rather short membranous cone. Epiproct not deep, broad, long based, with strongly down-curved long and sharp spine. Paraprocts with very wide base, otherwise slim, apical forth strongly curved dorsad and bearing a sharp spine. Subgenital plate oval. Cerci 14–16 segmented.

NYMPHS: 9·0–10·0 mm long (last instar, but not yet fully grown), greyish yellow to greyish brown without clear pattern. Head with some long hairs. Dorsal surface of body largely smooth; larger groups of spines along margins of pronotum; middorsal hairbrush on abdominal tergites I–X, one spine each side of it on posterior border of tergites I–IX.

AFFINITES AND DIAGNOSIS: *Trinotoperla groomi* Perkins is certainly a close ally of *T. minor* Kimmins and *T. minima* sp.n. Diagnostic characters of male *T. groomi* are the low, broad and long based epiproct with its strongly downcurved spine and the almost angulated paraprocts together with the lack of C–Sc crossveins.

DISTRIBUTION: *T. groomi* is known from several localities from northern to southern Queensland. In Crystal Cascades it is found sympatrical with *T. minor* Kimmins and *T. minima* sp.n., the two species considered its closest relatives.

TRINOTOPERLA MAIOR, sp.n. (Fig. 24 A–G)

MATERIAL. New South Wales: Holotype ♂ and 4 paratypes (3 ♂, 1 ♀), New England N.P., via Ebor, 22/23.i.1966, BKC; holotype (T.8523) and 1 paratype (♀) (T.8524) in QM, 2 paratypes (♂) in UQ, 1 paratype (♂) in GT. 2 paratypes (1 ♂, 1 ♀), Pt Lookout, via Ebor, 22.i.1967, BKC; in UQ. 2 ♂, 4 ♀, Dorrigo N.P., 30.i.1963, C.W. Frazier; in UNE. 2 ♂, 3 ♀, locality, date and collector unknown; in UNE.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	14·0–18·0	17·0–21·0
♀	16·0–21·0	19·0–23·0

Body largely greyish brown; black dots anteriorly on lateroventral edge and at base of coxa of meso- and meta-thorax; blackish brown at knees; all femora with pattern, and with well developed distal spur. Wings slightly suffused with whitish grey, greyish brown along all crossveins in forewing particularly in pterostigma area, only along pterostigma crossveins in hindwing. A set of C–Sc and 1A–2A crossveins in forewing, a few C–Sc crossveins in hindwing. Distal half of anal fan between 1A and 4A with rich irregular venation.

MALE GENITALIA (A–F): Tergite X produced into a short inconspicuous obtuse membranous cone. Epiproct with high and well expanded base, produced into a long strongly downcurved sharp

spine. Paraprocts of medium length, slender, slightly bowed, with rounded apices, a forward directed tooth about one fifth of their length from apex. Subgenital plate rather narrow, but well rounded apically. Cerci 16–19 segmented.

FEMALE GENITALIA (G): Subgenital plate wide with posterior border slightly concave; a very conspicuous black and strongly sclerotized M-shaped mark over almost its whole length and width. Paraprocts curved laterad, apices rounded. Tergite X produced medially into rounded apex. Cerci 16–20 segmented.

AFFINITIES AND DIAGNOSIS: *Trinotoperla maior* sp.n. is considered closely related to *T. nivata* Kimmins and *T. mouldsi* sp.n. It can be distinguished from these species by the distinctive epiproct and paraprocts in male and by the well defined black mark on the subgenital plate of the female.

DISTRIBUTION: *Trinotoperla maior* sp.n. is hitherto known only from New England and Dorrigo N.P., both localities in north-eastern New South Wales.

TRINOTOPERLA MINIMA, sp.n. (Fig. 25 A–G)

MATERIAL. Queensland: Holotype ♂ and 68 paratypes (35 ♂, 33 ♀), Palmerston N.P., Beatrice R, 27.vi.1971, EFR; 2 ♂, 3 ♀, Atherton Tableland, The Crater, 25.iv.1970, S.R. Curtis; 6 ♀, Crystal Cascades, nr Cairns, 10.vi.1971, EFR; 11 ♂, 13 ♀, Mossman Gorge, 16.vi.1971, EFR; 2 ♀, 2 km on Mt Edith Rd, Tinaroo Dam, 23.vi.1971, EFR; 6 ♂, 2 ♀, 40 km W. of Tully, 31.v.1971, EFR; 1 ♂, 2 ♀, Little Mulgrave R., 28.vi.1971, EFR; 10 ♂, 27 ♀, Upper Mulgrave R., via Gordonvale, 29/30.iv.1970, S.R. Curtis; all in ANIC. 5 ♀, Mena Ck nr Mt Utchee, 145°52'/17°40', 17.xi.1976, LM and GT; 2 ♂, 15
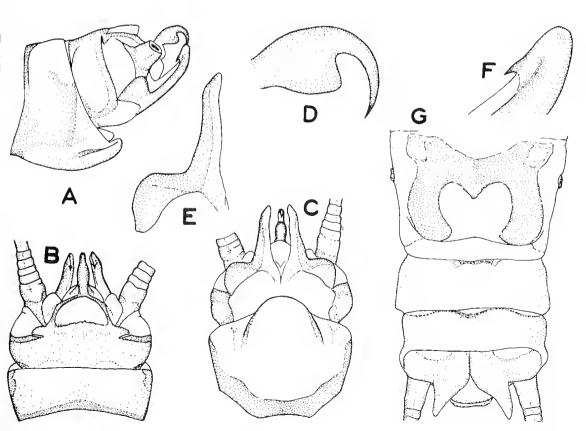

FIG. 24. *Trinotoperla maior* sp.n.: A–F, male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, epiproct, lateral view; E, paraproct, ventral view; F, tip of paraproct, lateral view; G, female genitalia, ventral view.

♀, Mossman Gorge, 145°52'/16°27', 19-25.xi. 1976, LM and GT; all in GT. 1 ♀, The Boulders, via Babinda, 15.xii.1966, BKC; 1 ♀, Crater N.P., Dinner Falls, 9.viii.1968, TW; 7 ♂, 4 ♀, Ringrose (= Crater) N.P., via Atherton, 9.xii.1966, BKC; all in UQ. Crystal Cascades, via Cairns: 1 ♂, 3 ♀, 30.xii.1963 and 2 ♀, 22.xii.1964, GBM; 1 ♀, 20.v.1966, D. Forno; 2 ♀, 8.viii.1966, GBM; 4 ♀, 6.xii.1966, GBM; all in UQ. 1 ♂, Kirrama State Forest, via Cardwell; 1 ♀, St. Lucia, 30.vi.1956, R. Howlett; 3 ♂, Zillie Falls, 12.viii.1968, TW; all in UQ. Upper Mulgrave R.: 1 ♂, 1 ♀, 1/3.xii.1965 and 1 ♂, 1 ♀, 30.iv.1970, GBM; all in UQ. Mossman Gorge: 5 ♂, 2 ♀, 10.viii.1969, TW; via Mossman, 23 ♀, 25/26.xii.1964, GBM; 13 ♂, 43 ♀, 7.xii.1966, BKC, and 1 ♂ 1 ♀, 2.vi.1971, BKC; all in UQ. Palmerston N.P.: 20 ♂, 20 ♀, 22.iv.1968, BKC; 2 ♂, 1 ♀, 25 nymphs, 8/12.viii.1968, TW; via Innisfail, 14 ♂, 16 ♀, 23.iv.1968, GBM; Henrietta Ck, 3 ♀, 5.xii.1965, GBM; all in UQ.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	8·0–10·0	8·5–10·5
♀	9·0–11·0	10·0–12·5

Dorsal surface of body and legs largely greyish brown, ventral surface pale yellow; pale yellow pattern on head and femora; black marks as described for *T. maior* sp.n.; distal spur minute on meso- and meta-femur, absent on profemur. Wings suffused faintly with greyish yellow, small greyish brown patches around all crossveins of forewing, larger reddish brown patches around pterostigma crossveins or indications of such in both wings. No C–Sc crossveins in anal fan.

MALE GENITALIA (A–E): Tergite X produced into a conspicuous subtriangular membranous cone. Epiproct short, slender, slightly S-curved, with pointed apex. Paraprocts of moderate length, slender, slightly bowed, with rounded apex, a forward directed tooth about one third of their length from apex. Subgenital plate of medium width, oval. Cerci with 11–13 segments.

FEMALE GENITALIA (G): Subgenital plate very wide and rather short, hind margin slightly incised medially and thus appearing bilobed. Paraprocts with swollen base and narrow rounded apex. Tergite X produced medially, but apex rounded. Cerci 10–14 segmented.
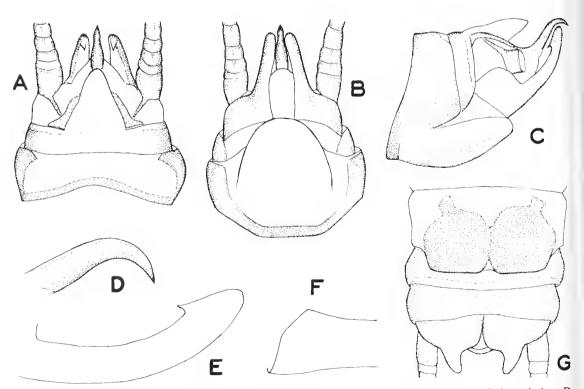

FIG. 25. *Trinotoperla minima* sp.n.: A–E: male: A–C, genitalia: A, dorsal view; B, ventral view; C, lateral view; D, epiproct, lateral view; E, paraproct without base, lateral view; F, G, female: F, apex of profemur, dorsal view; G, genitalia, ventral view.

NYMPHS: 8·0–9·0 mm long (last instar); body yellowish to dark brown with inconspicuous pattern on head prothorax and femora. Head with some long hairs. Dorsal surface of the body largely smooth; a few single spines along margins of pronotum; a median hairbrush on all abdominal tergites and one spine each side of it on posterior border of tergites I–IX.

AFFINITIES AND DIAGNOSIS: *Trinotoperla minima* sp.n. is closely allied with *T. minor* Kimmins from Victoria, New South Wales and Queensland, and *T. groomi* Perkins from Queensland. Both these species, however, are much larger than *T. minima* and have femoral processes in all legs while the forelegs of *T. minima* are unarmed. The differences between *T. minor* and *T. minima* in the genitalia, particularly the male, are not very substantial.

DISTRIBUTION: *Trinotoperla minima* sp.n. has hitherto been found in many localities, mainly smaller streams in tropical Queensland. Other *Trinotoperla* collected in the same habitats: *T. groomi, T. minor, T. mouldsi* sp.n.

TRINOTOPERLA MINOR Kimmins, 1951

T. minor was regarded a synonym of *T. nivata* Kimmins by Hynes (1974). As expressed and pointed out under *T. nivata* (q.v.) I believe that *minor* and *nivata* belong to different species groups within *Trinotoperla*.

MATERIAL. Victoria: 1 specimen, Lalal Falls, 15 mi. from Ballarat, 5.ii.1957, FAP; in UQ. 18 ♂, 5 ♀, Otways, Hopetown Falls, 18.ii.1970, EFR; in ANIC. New South Wales: Barrington House, via Salisbury: 1 ♀, 27.v.1963; 2 ♂, 1 ♀, 18.xii.1963; 1 ♂, 19.xii.1963, A. Macqueen; in UQ. 1 ♀, Ebor, 14.xii.1964, G. Wearne; in ANIC. 10 ♂, 56 ♀, Ebor Falls, 10.xi.1957, FAP; 1 ♀, Kiandra, 6.ix.1962, EFR; 1 ♀, Mt Kosciusko, 31.xii.1960, B. Willson; 1 ♀, Rocky Crossing, Williams R., via Salisbury, 27.v.1963, A. Macqueen; all in UQ. 1 ♂, 1 ♀, Serpentine R., 19/20.ii.1966, EFR; in ANIC. 1 ♂, Mulerindi, 10 km N. of Tamworth, 6.xi.1976, GT; 1 ♂, Shellbrook Ck nr Barrington Tops, 10.x.1976, LM and GT; 1 ♂, 2 ♀, Wollondilly R. nr Goodmans Ford, 6.x.1976, GT; all in GT. Queensland: Brisbane: 1 ♀, 20.vi.1949, T. Robertson; 1 ♀, 1958, students; 1 ♀, 4.v.1962, J. Miller; 1 ♀, Binna Burra, 20.v.1962, B. Bateman; 1 ♂, Christmas Ck, 10.vi.1967, P. Farlow; Crystal Cascades, via Cairns: 3 ♂, 5 ♀, ?.v.1962 and 1 ♂, 1 ♀, ?.v.1969, K. Korboot; 1 ♂, 2 ♀, Deep Ck, via Redlynch, ?.v.1963, K. Korboot; all in UQ. 1 ♂,

Flaggy Ck, Mistake Mts, via Laidley, 11.ii.1973, SRM; in UQ. 1 ♀, Gwongorella N.P., 6/7.xii.1976, GT; in GT. 1 ♀, Killarney, 9.v.1960, H. Dunston; 1 ♂, Killarney District, 3.iv.1955, N. Loveday; both in UQ. Lamington N.P.: 1 ♀, 30.v.1929, FAP; 1 specimen, 8.iv.1939, FAP; 1 ♂, ?.viii.1947, collector unknown; 2 ♀, 31.v.1955 and 1 ♂, 12 ♀, 1/5.vi.1955, FAP and ICY; 2 ♂, 8 ♀, 2/6.v.1956 and 1 ♀, 20.viii.1956, ICY; 1 ♀, 26.v.1959, E. Bernays; 1 ♀, 22.v.1962, A. Webb; 1 ♂, 11/17.ii.1963, A. Macqueen; 1 specimen, 17/21.v.1965, S.R. Curtis; all in UQ. 1 ♂, Mt Tamborine, 21.ix.1962, B. Andrews; 1 ♂, Natural Arch, Numinbah, 1.xi.1954, FAP; 1 ♂, R. Albert R., 17.ix.1958, S. Rigby; 1 ♂, Running Ck, via Beaudesert, 5.iii.1967, H. Buchanan; all in UQ.

TRINOTOPERLA MONTANA Riek, 1962 (FIG. 23 G)

T. montana, described from rich material of both adults and larvae by Riek (1962), was synonymized with *T. yeoi* Perkins by Hynes (1974). There is no doubt that these two names were given to very similar and probably closely related stoneflies. The discovery of the larva of *T. yeoi* (q.v.), however, brought to light a very significant character quite unique in the genus *Trinotoperla*. This, together with constant differences in the adults, which will be pointed out in detail elsewhere (Theischinger, in preparation, on *Trinotoperla*), in my opinion sufficiently justifies considering *T. montana* and *T. yeoi* as two separate species.

MATERIAL. New South Wales: As listed by Riek (1962) on p. 98.

TRINOTOPERLA MOULDSI, sp.n. (Fig. 26 A–H)

MATERIAL.. Queensland: Holotype ♂ (T.8525) and 1 paratype (♀) (T.8526), Ringrose (=Crater) N.P., via Atherton, 9.xii.1966, J. Goward; in QM. 2 ♀, Kirrama State Forest, via Cardwell, 16.xii.1966, BKC; 1 ♀, in UQ, 1 ♀, in GT. 1 ♀, Crater N.P., Dinner Falls, 9.viii.1968, TW; 1 ♀, Baldy Mtn Rd, 6 mls SW. Atherton, 1100 m, 27.xii.1972, BKC; both in UQ. 1 ♂, The Crater, nr Herberton, 6.i.1967, D.K. McAlpine and G. Holloway; 3 ♀, Kirrama State Forest, 24 km WNW. of Kennedy, 28.i.1981, M.S. and B.J. Moulds; all in AM.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	13·0	16·0
♀	15·0–17·0	18·0–20·0

Body coloured as described above for *T. maior* sp.n. Distal spur less prominent in meso- and meta-femur, minute to absent in profemur. Wings as in *T. maior* but pterostigma crossveins covered by extensive oval patches of dark reddish brown in both wings; only very few crossveins between 1A and 2A of forewing, generally no C–Sc crossveins and no anal crossveins in hindwing.

MALE GENITALIA (A–F): Central sclerite of tergite X produced posteriorly into a short very wide moderately deep membranous lobe. Epiproct with wide base and heavy, strongly downcurved hook. Papaprocts with very narrow base, otherwise bowed mediad with short, not much pointed apical hook, twisted inward. Subgenital plate oval. Cerci 16 segmented, inner basal sclerite not projecting.

FEMALE GENITALIA (G,H): Subgenital plate very wide with small median incision on hind margin, heavily sclerotized all over. Hind margin

of tergite X produced medially but apex well rounded. Paraprocts narrow, about as long as wide. Cerci with 13–15 segments.

AFFINITIES AND DIAGNOSIS: *Trinotoperla mouldsi* sp.n. is certainly closely related to *T. nivata* Kimmins and *T. maior* sp.n. It can be distinguished from both species by its narrow based paraprocts in both sexes.

DISTRIBUTION: *Trinotoperla mouldsi* sp.n. is hitherto known only from 3 localities in tropical Queensland: Kirrama State Forest, Baldy Mtn and Crater N.P. It coexists with *T. minima* sp.n. in Crater N.P.

TRINOTOPERLA NIVATA Kimmins, 1951

Hynes (1974) synonymized *T. minor* Kimmins and *T. groomi* Perkins with *T. nivata*. I do not believe, however, on the evidence of the material
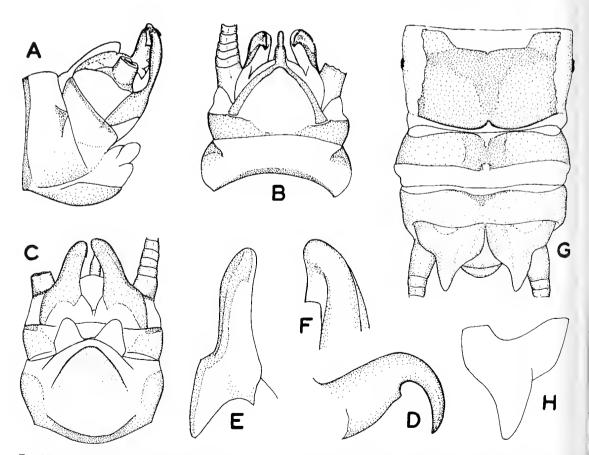
FIG. 26. *Trinotoperla mouldsi* sp.n.: A–F, male: A–C, genitalia: A, lateral view; B, dorsal view; C, ventral view; D, epiproct, lateral view; E, paraproct, ventral view; F, tip of paraproct, lateral view; G, H, female: G, genitalia, ventral view; H, paraproct, ventral view.

from southern New South Wales and Victoria I have hitherto seen, that *T. nivata* and *T. minor* are one and the same. Moreover, on the evidence of rich material from northern New South Wales and Queensland, I think that *T. minor* and *T. nivata* belong to different species groups even if eventually areas will be found where they interbreed.

I regard as *nivata* group (C–Sc crossveins present) *nivata* Kimmins, *maior* sp.n. and *mouldsi* sp.n. and as *minor* group (no C–Sc crossveins) *groomi*, *minima* sp.n., *minor* Kimmins and *sinuosa* sp.n. There is no doubt that *maior*, *mouldsi* and *sinuosa* are different from *nivata* and *minor* or from possibly interbreeding populations on morphological reasons. That *groomi*, *minor* and *minima* coexist for example at Crystal Cascades (Queensland) leaves little doubt about their specific distinctness from each other.

T. nivata was illustrated in detail by Hynes (1974) in Fig. 13 (right). Apart from the C–Sc crossveins I found the strongly developed inner sclerotization at the cercus base a good character for the identification of *T. nivata* males (well figured by Hynes).

MATERIAL. Victoria: 1 ♂, 8 ♀, Gunyah, March 1956, G. Bornemissa; in ANIC. 4 ♂, 1 ♀, Mt Bogong-Tawonga, 31.xii.1976, GT; in GT. 1 ♂, Warburton, 2.viii.1967, TW; in UQ. New South Wales: 1 ♂, 4 ♀, Fitzroy Falls, 22.iii.1961, EFR; 1 ♀, Kiandra, 17.ii.1961, EFR; all in ANIC. Mt Kosciusko: 1 ♀, 10.ii.1980, GT; 7 ♂, 20 ♀, Diggers Ck, 1200m, 10.ii.1980, C., D. and G. Theischinger; 1 ♂, 1 ♀, Perisher Ck, 1500m, 10.ii.1980, GT; all in GT. 1 ♂, Blue Mts, Wentworth Falls, Leura, 13.xii.1959, P.R. Webb; in UQ.
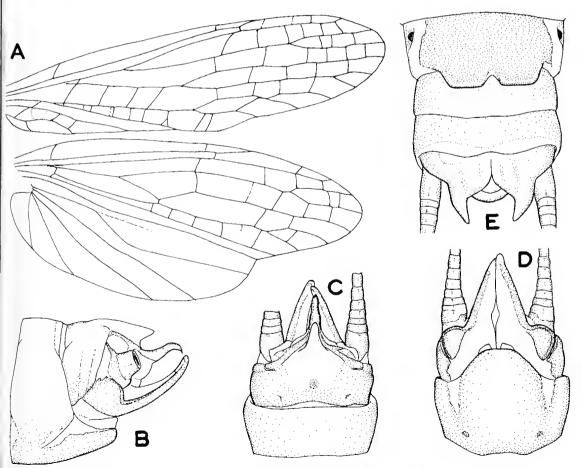
FIG. 27. *Trinotoperla sinuosa* sp.n.: A–D, male: A, wings; B–D genitalia: B, lateral view; C, dorsal view; D, ventral view; E, female genitalia, ventral view.

TRINOTOPERLA SINUOSA, sp.n. (Fig. 27 A–E)

MATERIAL. Victoria: Holotype ♂, 2 paratypes (1 ♂, 1 ♀) and 15 nymphs, Mt Langi Ghiran, 17.xii.1966, EFR; 1 ♀, Mt Buangor, 17.xii.1966, EFR; all in ANIC. 1 ♂, locality, date and collector unknown; in GT. 1 ♂, McKenzie Falls, 11 mi. from Halls Gap, 6.ii.1957, FAP; in UQ.

ADULTS: Measurements (in mm):

	Body	Forewing
♂	10·5–13·5	10·5–14·5
♀	13·0–15·0	15·0–16·5

Body and legs largely yellowish grey to dark brown, indistinctive brownish yellow pattern on head and on femora. Distal spur on all femora. Wings (A) slightly suffused with greyish brown, darker between C and R and along all crossveins of forewing. No C–Sc crossveins; a few crossveins between 1A and 2A in forewing; no crossveins in anal fan, 2A strongly sinuous in hindwing.

MALE GENITALIA (B–D): Tergite X produced into a narrow slender membranous process. Epiproct short with base hardly expanded and pointed apex. Paraprocts of medium length, slightly bowed and tapered without any tooth. Subgenital plate long and wide, oval. Cerci 18–19 segmented.

FEMALE GENITALIA (E): Subgenital plate rather narrow with deep medial incision on hind margin. Paraprocts with broad base and narrow tapered apex. Hind margin of tergite X produced medially but apex rounded. Cerci 17–18 segmented.

NYMPHS: 12·0–13·5 mm long (last instar); dorsal surface greyish brown, ventrally yellowish grey. Head without long hairs. Dorsal body surface, particularly abdominal tergites, largely covered with many scattered spines; one slightly larger spine each side and close to midline on posterior border of tergites I–IX; a barely developed median hairbrush on all abdominal tergites.

AFFINITIES AND DIAGNOSIS: *Trinotoperla sinuosa* sp.n. is certainly closely related to *T. minor* Kimmins, *T. groomi* Perkins and *T. minima* sp.n. It can be distinguished from all of them by the strong arch of 2A in the hindwing of both sexes. Additionally the male stands out by entirely unarmed narrow based paraprocts, the female by a definitely bilobed subgenital plate.

DISTRIBUTION: *Trinotoperla sinuosa* sp.n. seems to be restricted to the southwest of Victoria.

TRINOTOPERLA WOODWARDI Perkins, 1958

Though refraining from formally suggesting that *T. woodwardi* is a synonym of *T. irrorata* Tillyard, Hynes (1974) expressed that he personally had little doubt that these two large species are one and the same. Having studied the holotype and all other available material of *T. woodwardi* as well as a fine series of *T. irrorata* from different localities in southern New South Wales I have no doubt at all that they are distinct on specific level. Details of the genitalia of both species have been figured already reasonably well and correctly by Perkins (1958), McLellan (1971) and Hynes (1974).

MATERIAL. Queensland: As listed by Perkins (1958) on pp. 93, 94.

TRINOTOPERLA YEOI Perkins, 1958 (Fig. 23H)

T. yeoi, described from Lamington National Park in Queensland, was considered the older synonym for *T. montana* Riek by Hynes (1974). Plentiful material of *T. yeoi* from Queensland and New South Wales, particularly the discovery of its larvae, however, made me consider *T. montana* and *T. yeoi* as two distinct species. Only the larva of *T. yeoi* is characterized below while the imaginal characters of *T. montana* and *T. yeoi* will be pointed out in detail elsewhere (Theischinger, in preparation, on *Trinotoperla*).

MATERIAL. New South Wales: 10 ♂, 6 ♀, 33 nymphs, Allyn R., nr Barrington Tops, 18.viii.1980, GT; in GT. Queensland: As listed by Perkins (1958) on pp. 95, 98. 12 nymphs, Lamington N.P., 20.viii.1956, ICY; in UQ.

NYMPHS: 10·5–12·5 mm long (last instar); dorsally greyish brown, ventrally pale greyish yellow; pale whitish yellow pattern on femora. Dorsal body surface clothed with scattered short spines; a faintly developed hairbrush along midline of abdomen; conspicuous conical swellings, beset with many small spines on top, each side on pronotum.

LITERATURE CITED

HYNES, H.B.N., 1974. Comments on the Taxonomy of Australian Austroperlidae and Gripopterygidae (Plecoptera). *Aust. J. Zool., Suppl.* 29: 1–36.
    1976. Tasmanian Antarctoperlaria (Plecoptera). *Aust. J. Zool.* 24: 115–43.

KIMMINS, D.E., 1951. A revision of the Australian and Tasmanian Gripopterygidae and Nemouridae (Plecoptera). *Bull. Brit. Mus. nat. Hist. Ent.* **2**: 45–93.

MCLELLAN, I.D., 1971. A revision of the Australian Gripopterygidae (Insecta: Plecoptera). *Aust. J. Zool., Suppl.* **2**: 1–79.

PERKINS, F.A., 1958. Australian Plecoptera. Part I. Genus *Trinotoperla* Tillyard. *Pap. Dep. Ent. Univ. Qld* **1**(6): 85–100.

RIEK, E.F., 1962. A new genus of Australian stoneflies (Plecoptera: Gripopterygidae). *Proc. Linn. Soc. N.S.W.* **87**: 96–8.

THEISCHINGER, G., 1980. New stoneflies (Plecoptera) from New South Wales, Australia. *Aquatic Insects* **2**: 249–56.

—— 1981. New and little known stoneflies from Australia (Insecta: Plecoptera). *Aquatic Insects* **3**: 103–27.

TILLYARD, R.J., 1921. The wing venation of the Leptoperlidae (Perlaria) with description of a new species of the genus *Dinotoperla* from Australia. *Trans. R. Soc. S.Aust.* **45**: 270–4.

—— 1924. New genera and species of Australian stoneflies (order Perlaria). *Trans. R. Soc. S.Aust.* **48**: 192–5.

Hynes (1978) in "An annotated key to the nymphs of the stoneflies (Plecoptera) of the State Victoria" (Aust. Soc. Limnol. Spec. Pubn. 2, 1-63), a publication that did not become available to me before submission of the manuscript of the above paper, realizes that he was wrong when synonymizing *Dinotoperla fontana* Kimmins with *D. serricauda* Kimmins (Hynes 1974). He maintains, however, his view (Hynes 1974) on the synonymy of the other *Dinotoperla* and of the *Illiesoperla* and *Trinotoperla* species as recorded above. Under *Trinotoperla nivata* Kimmins he comments on the possible existence of an undescribed *Trinotoperla* in the Grampians the female of which he had already figured (Hynes 1974, under *T. nivata*). This species is no other than *T. sinuosa* sp.n. as described above.

A BLIND TERRESTRIAL WATER BEETLE
FROM AUSTRALIA

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ABSTRACT

Terradessus caecus, a new genus and species of hydroporine Dytiscidae is described from a mountain top in North Queensland. The species lives in rainforest litter and lacks eyes and most swimming modifications.

INTRODUCTION

In 1979 Brancucci (1979) described a small dytiscid beetle from the floor of primary forest at altitudes of between 1700 m and 2150 m in the southern Himalayas. This was the first reported discovery of a terrestrial dytiscid. I describe here a second genus and species of terrestrial dytiscid, from Australia. Like the Indian species it is very small and was found on the floor of high altitude forest. In addition it is blind.

Terradessus gen. nov. Dytiscidae-Hydroporinae

Small, flattened, wingless and eyeless. Head lacking raised clypeal margin or cervical stria. Pronotum without striae, wider than elytra. Plane of anterior ventral surface of prothorax not greatly different from plane of prothoracic process and rest of ventral surface. Metacoxal plate and first abdominal segment fused. Elytra fused, without striae. Metatrochanters large, widely separated, exposed. Metatibia slightly arcuate, slightly narrower at base. Pro- and mesotarsi with segments 1–3 swollen, segment 4 minute. Metatarsus undifferentiated. Meta- and mesotibia with many short stout spines, lacking swimming hairs. Parameres asetose.

TYPE SPECIES : *Terradessus caecus* n.sp. (Plate 1, A–F)

Small (1·3 mm long, 0·7 mm wide), flattened, elytral edges subparallel, roundly narrowing in posterior third. Brown, edges of pronotum and appendages a little lighter. Head broad, evenly but sparsely punctured by small sharp punctures, finely reticulate. Pronotum broad with even, well-marked lateral flanges, longer in midline; punctures as on head except for a few larger ones along anterior margin and a general enlargement toward posterior angles, strongly reticulate as on head. Elytra flattened, extreme anterior angles flanged, lacking margined epipleural pits, epipleurae narrow, widening beneath anterior elytral flanging, reticulate, strongly and evenly punctate, slightly weaker towards midline anteriorly, without striae. Underside reticulate, strongly and deeply punctured. Legs stout, metatrochanters large. Metacoxal lines weakly raised, widely separated, subparallel, diverging in anterior third. Prothoracic process long, narrow. Apical segments of antenna slightly enlarged.

MALE: Pro and meso claws slightly stronger than in female. Aedeagus simple, widest a little posterior to apex which is bluntly pointed, dorsal surface with broad midline groove.

SPECIMENS EXAMINED: Holotype ♂ (Queensland Museum, T.8505) Queensland (NEQ) Mt. Sorrow summit, Cape Tribulation, 19.x.1980, G.B. Monteith, Q.M. BERLESATE No. 262, 16·08 S, 145·26 E, rainforest, 800 m. Sieved litter. Allotype and 6 paratypes same data, 9 paratypes same data except BERLESATE No. 261. All specimens are in the Queensland Museum, except two paratypes in the author's collection, two paratypes in the Australian National Insect Collection, Canberra, and one paratype in the British Museum.

DISTRIBUTION.

The only known locality is the top of Mount Sorrow in North Eastern Queensland.

RELATIONSHIPS.

Although *T. caecus* clearly belongs to the subfamily Hydroporinae to which tribe, if any, it belongs is not clear. I have placed it in the Bidessini on the grounds of its very small size, its fused metacoxal plate and first abdominal segment and its simple aedeagus. It is unusual among the Bidessini in the strongly reticulate surface, weakly deflexed prosternal process, lack of pronotal and elytral striae and in having the hind tibia not greatly narrowed basally as in many genera in the Bidessini. In some of these characters it resembles the Hydroporini, in particular *Paroster*. The surface sculpture is typical of *Paroster* as is the narrow prothoracic process, spined mesotibia, broad metacoxal process, large exposed metatrochanters and simple aedeagus.

Its small size, widened rather than narrowed pronotal base, lack of any trace of elytral grooves and simple aedeagus separates it from the Carabhydrini.

In many aspects *Terradessus* resembles the Bidessini genus *Geodessus* recently described from Northern India and Nepal (Brancucci, 1979). *Geodessus* is also terrestrial, devoid of dorsal striae, lacks swimming hairs and is very small (1·5 mm). From the figures and description it differs from *Terradessus* in many small points. Unlike *Terradessus, Geodessus* has well-developed eyes. The keys to Australian Dytiscidae given in Watts (1978) will not accommodate *Terradessus* below the subfamily level. The genus, however, is readily recognized by its lack of eyes and very small size. Ordish (1976) has described two blind genera of minute Bidessini from subterranean waters in New Zealand, viz. *Kuschelhydrus* and *Phreatodessus*. Both these genera differ markedly from *Terradessus* by their constricted pronotal base, their long setae on elytra and pronotum, and their normal fringe of swimming hairs on the hind legs. *Terradessus* differs from the blind, subterranean hydroporine genus, *Morimotoa*, described by Uéno (1957) from Japan by its lack of swimming fringes on legs and dorsal setae.

HABITS.

Little is known of the life history of this intriguing dytiscid. All specimens were collected by berlese extraction of leaf litter from the rainforest floor. Although the area is one of high rainfall and high fog precipitation, the area the beetles were collected from was devoid of standing water and they cannot be considered aquatic. Eyelessness is most often associated with a subterranean existence. Flightlessness is more ˀmmon but could also be associated with a terranean lifestyle. On the little evidence a ˡable, it is perhaps most likely that this minute, flattened dytiscid is adapted to live deep within leaf litter that is wet for much of the time and damp for most. Judging by the number collected the beetles are quite common in this environment. Whether or not the larvae also live in this environment is unknown but it would be surprising if they did not.

Terradessus and *Geodessus* seem to be exploiting a similar niche and detailed comparisons between the two genera would be interesting. Between Nepal and Australia there are many similar habitats which could well yield more examples of reinvasion of the land by dytiscid beetles. The presence of *Terradessus caecus* on Mount Sorrow is undoubtedly another example of the disjunct, relict insect fauna of these wet North Queensland mountain tops referred to by Monteith (1980).

ACKNOWLEDGEMENTS

LITERATURE CITED

BRANCUCCI, M., 1979. *Geodessus besucheti* n. gen., n.sp. le premier Dytiscide terrestre (Col., Dytiscidae, Bidessini). *Ent. Basiliensia* **4:** 213–8.

MONTEITH, G.B., 1980. Relationships of the genera of Chinamyersiinae, with description of a relict species from mountains of North Queensland. (Hemiptera: Heteroptera :Aradidae). *Pacific Insects* **21:** 275–85.

ORDISH, R.G., 1976. Two new genera and species of subterranean water beetle from New Zealand (Coleoptera:Dytiscidae). *New Zeal. J. Zool.* **3:** 1–10.

UÉNO, S.–I., 1957. Blind aquatic beetles of Japan, with some accounts of the fauna of Japanese subterranean waters. *Arch. Hydrobiol.* **53:** 250–96.
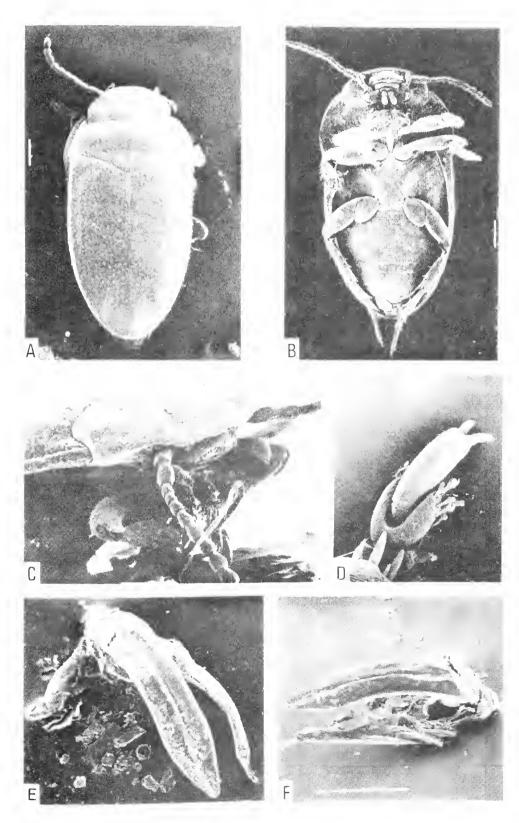
WATTS, C.H.S., 1978. A Revision of the Australian Dytiscidae (Coleoptera). *Aust. J. Zool. Suppl. Series,* **57**.

PLATE 1
TERRADESSUS CAECUS GEN. ET. SP. NOV.
A. Dorsal view.
B. Ventral view.
C. Head and mouthparts.
D. Dorsal view of fore tarsus.
E. Aedeagus and paramere, dorsal view.
F. Aedeagus and paramere, ventral view.
(All scale lines equal 100 μ.)

DRY SEASON AGGREGATIONS OF INSECTS
IN AUSTRALIAN MONSOON FORESTS

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ABSTRACT

Observations are recorded on aggregation behaviour by insects in monsoon forest patches in tropical Australia during the dry winter months. Species of the Hemiptera, Lepidoptera and Diptera were involved, some of which normally inhabit open forest but which migrate into the monsoon forest patches to form aggregations. The behaviour is interpreted as having a group defence function whereby natural defences of distastefulness, repugnatorial glands or buzzing behaviour are reinforced by massed individuals.

INTRODUCTION

The northern third of Australia experiences a tropical monsoon climate with a pronounced wet season occurring during the summer months of December to April under the influence of the northwest monsoon air flow. Typically, the rest of the year is very dry. This highly seasonal rainfall pattern is not normally adequate to support true tropical rainforest (closed forest) except in areas where the monsoonal rains are augmented by other rain systems which reduce the impact of the monsoonal dry season. This only occurs along the eastern seaboard of Queensland where the combined effect of a moist southeast airflow off the Pacific Ocean and the orographic influence of subcoastal mountains yields the necessary rains for fully developed evergreen rainforest. However, in the remainder of the tropical zone several types of closed canopy forest occur which are floristically and structurally similar to true rainforest but are usually referred to as 'monsoon forest' because of their lower plant diversity and tendency to deciduousness in the dry season. They include several of the structural categories of Australian rainforests defined by Webb (1978). They can be regarded as a type of rainforest which has developed under extreme seasonality of rainfall. Monsoon forests in Australia are very limited in area and occur as small patches and strips in favourable locations in Cape York Peninsula, the 'Top End' of the Northern Territory and the Kimberleys. Their boundaries are clearly defined and they generally stand in marked contrast to the open eucalypt/melaleuca forests and woodlands which surround them.

During the hot, dry season conditions in the open forests are extremely harsh and the pockets of shady, moist monsoon forest become important refuges for many animal species. This is conspicuous in the grazing mammals, for instance, and in the Northern Territory the monsoon forest patches are shelters for wallabies and feral buffalo, pigs and cattle which feed in adjacent grasslands. This behaviour is poorly documented among the insects but recent observations by the author during a collaborative project (Kikkawa and Monteith, 1980) indicate that some butterfly species normally restricted to open forest shelter in the monsoon forests during the dry season (e.g. *Acraea andromacha* (Fabricius) *Danaus chrysippus* (Linnacus), *Junonia orithya* (Linnaeus)). A remarkable related phenomenon is the formation of massive aggregations of certain insect species which persist in a semiquiescent state for several months in these monsoon forests during the dry season. This behaviour has received only cursory mention in the Australian literature. The present paper presents new field observations on this behaviour, summarizes the sporadic literature and discusses the possible significance of these aggregations.

RECORDS OF INSECT AGGREGATIONS FROM AUSTRALIAN MONSOON FORESTS

In the following account insect species are discussed systematically under order and family. Where no other source is cited the observations were made by the writer. Most of these were made during a 4 week visit to the Northern Territory in July, 1979, during which insect surveys were conducted in eleven monsoon forest patches. In nine of these, insect aggregations were encountered. The localities and the insect species concerned are tabulated in Table 1.

HEMIPTERA : SCUTELLERIDAE

Lampromicra senator (Fabricius) 1803

On May 21, 1972, clusters of up to 50 individuals of this metallic green species were found hanging from shrub foliage in gallery monsoon forest along Beame's Brook, 30 km SW of Burketown, Gulf of Carpentaria. The insects were tightly packed, semiquiescent and showed little inclination to disperse when disturbed. At the same site crow butterflies (*Euploea core* Cramer) were also aggregating. McDonald (1963) records *Lampromicra senator* in southern Queensland as breeding on the shrub *Breynia oblongifolia* in open forest and hibernating as adults in winter in various concealed situations. At Beame's Brook the clusters were quite exposed and occurred on several species of plants, not all of which could have been *Breynia*. It is assumed that the bugs had migrated into the monsoon gallery forest to pass the dry winter. In southern Queensland another scutellerid, *Cantao parentum* (White), undergoes mass over-wintering, adult clustering, often on non-host plants to which it migrates (McDonald, 1963; pers. obs.)

HEMIPTERA : ALYDIDAE

Leptocorisa acuta (Thunberg) 1783

This slender, grass-feeding bug is widespread in northern Australia and may become a pest of rice. Its biology in Papua New Guinea has been studied by Sands (1978). In the Northern Territory it was found aggregating in five of the monsoon forest patches in July (Table 1), particularly at Kemp Airstrip where enormous numbers occurred (Plate 1C). At none of the sites were grasses, the normal foodplant, present. The insects rested quietly in clusters beneath leaves or in rows along twigs and petioles of low shrubs and ferns, never more than a metre above the ground. When disturbed the clusters burst into buzzing, brief flight, discharging their repellent scent glands, before settling

again in the original site. Sands (1978) describes a pattern of behaviour in this species in Papua New Guinea where onset of dry weather triggers migration from open grassland to shaded sites where gregarious aestivation for up to two months takes place. He noted heavy egg mortality during dry weather and interpreted the migration-aestivation behaviour of adults as a reproductive strategy to counter this. Undoubtedly the clustering seen in monsoon forests of Northern Australia is the same phenomenon, but with a much longer dry season the period of aestivation there probably reaches 5–6 months.

Noliphus erythrocephalus Stal

This species was noted clustering with *Leptocorisa acuta* at the Kemp Airstrip forest in July (Table 1), where it was greatly outnumbered by *L. acuta*. Similar mixed clusters of *Leptocorisa* and *Noliphus* have also been noted in gallery monsoon forest along the Stewart River in Cape York Peninsula in late June, 1976. At the latter site some pure clusters of *Noliphus* were observed (Plate 1B). Like *Leptocorisa acuta, Noliphus erythrocephalus* appears to be principally an open forest species and thus this clustering activity away from the normal habitat is probably a similar migration-aestivation behaviour to that described for *Leptocorisa*.

HEMIPTERA : COREIDAE

Gralliclava australiensis Dolling, 1978

This small bug is distributed across the tropical north of Australia (Dolling, 1978) where it feeds on pods of leguminous herbs such as *Crotalaria* spp., principally in open forest. In July, 1979, it was found in considerable numbers in four lowland, monsoon forest patches in the Northern Territory (Table 1). It occurred there in small clusters, usually of no more than six individuals, in concealed situations such as rolled dead leaves, abandoned spider retreats among shrub foliage and among leaf litter on the ground. The insects in these small clusters were semiquiescent when disturbed and reluctant to disperse but eventually discharged their repugnatorial glands. At the time of observations no suitable foodplants for the bugs occurred inside the monsoon forest patches, and in the surrounding open forest where foodplants did occur there were no apparent *Gralliclava*. For this reason it is assumed that populations of bugs had migrated into the monsoon forest patches.

TABLE 1: PRESENCE OF AGGREGATIONS OF INSECT SPECIES OBSERVED IN 9 MONSOON FOREST TRACTS IN THE NORTHERN TERRITORY DURING JULY, 1979.

SPECIES	Mt. Gilruth Gorge 13·02Sx133-05E	Radon Creek 12-45Sx132-53E	Cahills Crossing 12·25Sx132-58E	South Alligator R. 12-40Sx132-30E	West Alligator R.(1) 12·12Sx132-13E	West Alligator R.(2) 12-11Sx132-16E	Kemp Airstrip 12·35Sx131-20E	North Point 12·25Sx132-22E	Ininowinyin Gorge 12-23Sx133-03E	Favoured Aggregation Sites
Coptosoma lyncea (Hemiptera: Plataspidae)			X							tree foliage
Noliphus erythrocephalus (Hemiptera:Alydidae)							X			low herbage and grasses
Leptocorisa acuta (Hemiptera:Alydidae)			X	X	X	X	X			low herbage and grasses
Gralliclava australiensis (Hemiptera:Coreidae)				X	X	X		X		in curled leaves and litter
Euploea core (Lepidoptera:Nymphalidae)		X	X	X	X		X	X		trunks and roots of 'banyan' fig trees; sheltered rock faces; tree foliage
Euploea sylvester (Lepidoptera:Nymphalidae)		X	X	X	X		X	X		trunks and roots of 'banyan' fig trees; sheltered rock faces; tree foliage
Danaus affinis (Lepidoptera:Nymphalidae)					X					tree foliage
Euphumosia papua (Diptera:Calliphoridae)	X	X	X						X	sheltered rock faces near water
Pericyna sp. (Diptera:Dolichopodidae)	X									base of tree trunks
sp. indet. (Diptera:Milichiidae)	X									foliage hanging over stream bed
Totals	3	3	5	4	5	2	4	3	1	

HEMIPTERA : PLATASPIDAE

Coptosoma lyncea Stal

This stink bug was found in one very large aggregation and in several smaller clusters on broad-leaved trees at one monsoon forest locality in the Northern Territory in July, 1979 (Table 1). Several species of trees were involved so it is assumed that at least some of the aggregations were not on foodplants of the bug. The largest aggregation occurred on a tree about 5 m in height, of which every single leaf was covered with bugs (Plate 1D). The bugs assumed a regular spacing on the underside of leaves and in rows along the petioles, giving the initial impression of being a natural pattern of galls or blemishes on the plant. The insects rested immobile when undistrubed and none were seen to feed on the plant. When disturbed, large numbers of bugs took flight instantly, accompanied by loud buzzing and by discharge of stink glands. After several minutes all returned to their original roosting tree and became quiescent again.

DIPTERA : DOLICHOPODIDAE

Sympycnus sp. cf. *apicalis* de Meijere

This small, long legged fly was found in several aggregations on the base of tree trunks in monsoon forest at the bottom of a gorge near Mount Gilruth in July, 1979 (Table 1). The flies formed dense-packed carpets of individuals, usually ovate in shape and up to about half a square metre in area. When disturbed they were reluctant to take flight and soon settled into a quiescent swarm again. It is not known whether monsoon forest is the normal habitat of this species.

DIPTERA : MILICHIIDAE

gen. & sp. indet.

One cluster of this tiny black species was observed on low hanging foliage above the dry creek bed in a deep shady part of the gorge at Mt. Gilruth (Table 1). The flies densely covered several terminal leaves of a branch and were normally immobile (Plate 1A). When disturbed, the flies exhibited mass flight activity accompanied by high pitched buzzing before eventually settling down again on the original leaves. This cluster was above a path used by our collecting party and was disturbed many times during the 3 days work at that locality, but it never moved from its site. The flight buzzing closely resembled that of a disturbed wasps' nest and is thought to be defensive. It is not known if monsoon forest is the normal habitat of this species.

DIPTERA : CALLIPHORIDAE

Euphumosia papua Guérin - Meneville

This large, strikingly-coloured blowfly was recorded from Arnhem Land by a previous survey (CSIRO, 1975) and their report comments on its commonness in sandstone areas. Its breeding habits are unknown but Ferrar (1978) descibed the larvae. In July, 1979, it was noted aggregating at 4 sites in Arnhem Land (Table 1), always on shaded rockfaces and usually near water. Groups of up to several thousand individuals occurred, resting quietly and were sluggish when disturbed and reluctant to fly.

LEPIDOPTERA : NYMPHALIDAE

Euploea core corinna (W.S. Macleay) 1826

The Common Crow is a ubiquitous butterfly of northern and eastern Australia where it is principally an open forest species. Like most other danaines its larvae feed on toxic plants and the adults are considered to be distasteful to birds. There are a number of passing remarks in the literature concerning sightings of aggregations of

this species but these do not appear to have been summarized. In the following they are treated, together with various unpublished observations, geographically by States:

QUEENSLAND: Alexander (1933) records a roosting site near Westwood 45 km W of Rockhampton. The aggregation occurred in *Casuarina* trees on a creek bank and some butterflies occupied the site at all times of the day. Alexander notes that the roosting site seemed active at all times of the year during his 3 years' residence at Westwood. McCubbin (1971) writes that this species 'congregates during winter at various places around the coast. Large numbers collect in sheltered gullies on some Barrier Reef islands including Lindeman Island, Hayman Island, Brampton Island and Magnetic Island.' McCubbin also records observations of J.C. LeSouef that 'hundreds gather during winter on bamboo clumps in both Rockhampton and Darwin gardens.' Monteith (1972) records clusters of the species on *Pandanus* foliage in gallery forest along Beames Brook near Burketown on May 21, 1972. A map accompanying Anonymous (1974) shows an aggregation site for *Euploea core* seen in August, 1973 at the bottom of a sandstone gorge in the Isla Gorge National Park, near Theodore. Unpublished observations of aggregations in Queensland are those by M. DeBaar (pers. comm.) of clusters in clefts between boulders at Laura Gorge in June, 1978, and by R. Molnar and G. Czechura (pers. comm.) of massed butterflies on rock overhangs and trees at the bottom of Porcupine Gorge, near Hughenden, in June 1980. Three occurrences of these aggregations of *Euploea core* have been witnessed by the writer in Queensland. The first was on May 23, 1968, when a dense roost of between two and four thousand individuals was encountered on several shady trees clumped together on the bank of Major's Creek, at the western base of Mt. Elliot, near Townsville. The second was in June, 1971, when a very large aggregation was seen extending for about 50 metres on dense, shady trees overhanging a dry anabranch channel of the Coen River, near Coen township. The third was in June 1971, at a sandstone outcrop 30 km west of Fairview, near Laura, where small quiescent clusters of butterflies occurred on cool, shaded rockfaces around the base of the outcrop.

NORTHERN TERRITORY: McCubbin's (1971) mention of LeSouef's observation of *Euploea core* aggregating on bamboo clumps in Darwin gardens has already been noted. LeSouef (1971) records

having seen many hundreds resting in a patch of 'Jungle' (= monsoon forest) along the Daly River in June, 1970. S. and K. Breeden (1975), writing on the sandstone massifs of Arnhem Land in May, illustrate a cluster of this species on a twig and state that 'hundreds of these butterflies crowd together in dark corners of the escarpment's rainforests'. During the writer's visit to Northern Territory in July, 1979, aggregations of this butterfly were found in six of the nine monsoon forest patches studied (Table 1). One of these was in a gorge in the Mount Brockman sandstone (Radon Creek) where the butterflies rested on shaded, overhanging rockwalls at the head of the gorge. The remaining five aggregation patches were on the plains where the monsoon forest occurred either as gallery strips along watercourses (South Alligator, Cahill's Crossing) or as small isolated patches surrounded by open sclerophyll forest (West Alligator 1, Kemp Airstrip, North Point). At these plains sites aggregation foci were provided by the interwoven roots and trunks of the giant 'banyan' fig trees, *Ficus virens*, where the dense shade given by their evergreen crowns yielded the coolest, darkest part of the forest (Plate 1E & F). All these aggregations behaved similarly. The butterflies rested quietly, with heads upwards, but were quite alert. When approached there appeared to be a critical distance after which a small group of butterflies suddenly launched into swirling flight. This activity had a chain reaction effect, triggering others until the whole swarm joined the flight. Then slowly they settled back into their original positions until within a couple of minutes all were quiet again.

WESTERN AUSTRALIA: Bailey and Richards (1975) describe 'large and spectacular aggregations' of *Euploea core* in mangroves at King Cascade and on rock faces in vine thicket at Enid Falls during August, 1974. Both these localities are in the Prince Regent River region of the Kimberleys which is more or less the western limit of the species' range in Australia.

Euploea sylvester (Fabricius), 1793
Two subspecies of the species occur in Australia, *E. sylvester sylvester* (F.) along the eastern Queensland coast and *E. sylvester pelor* Doubleday and Hewitson, 1847 in the north of the Northern Territory and the Kimberleys of Western Australia. Aggregation behaviour has been recorded in both subspecies. Kershaw (1915) describes *E. s. sylvester* in the monsoon forest at

Iron Range, in Cape York Peninsula, in November 1913 where 'hundreds . . . . . were flying about, while dozens could be seen resting on a single dead tree, several being taken with one sweep of the net.' In the Northern Territory the writer recorded *E. s. pelor* as a minor component of all of the clusters of *Euploea core* noted (Table 1). Specimens of *E. sylvester* were hard to distinguish from *E. core* when resting or flying but from captures it is estimated that they never exceeded about 5% of the aggregations. They indulged in the same flight activity described for *E. core* above.

Euploea tulliolus tulliolus (Fabricius) 1793
The only record of an aggregation is that of Waterhouse (1932) who says that 'on Lindeman Island, near Mackay, I once saw this butterfly in hundreds settled on the trees in a shaded gully, and was able to catch many specimens with one sweep of the net.'

Euploea eichhorni Staudinger, 1884
M. DeBaar (pers. comm.) records this species aggregating with *Euploea core* in shaded clefts between boulders at Laura Gorge in June, 1978.

Danaus affinis affinis (Fabricius) 1775
This species is often very common in coastal situations across northern Australia. At one of the sites surveyed in the Northern Territory in July, 1979, it was found resting in numbers with aggregating *Euploea core* (Table 1). However, the *D. affinis* were much less quiescent than the *Euploea* spp. and random flight activity took place.

Danaus hamatus hamatus (W.S. Macleay) 1826
This butterfly occurs across northern Australia and down the east coast. In some years it builds up to large numbers during summer and migrations may occur along the coast during the autumn. During these migrations large concentrations of butterflies may build up on capes, headlands and some off-shore islands. Such concentrations were observed and commented on by some of the earliest explorers. For example, on Cook's first voyage along the east coast in 1770, on May 29 at Thirsty Sound, they found 'butterflies . . . . the air was for the space of 3 or 4 acres crowded with them to a wonderful degree . . . . yet every branch and twig was almost covered with those that sat still' (Banks, 1962). Later, Phillip Parker King (1826) noted similar swarms at Cleveland Bay in

June, 1819, 'as well as every other place we had landed upon within the tropic'. In more recent time McNeil (1937) noted an enormous camp on Hayman Island in May, 1933, which dispersed for feeding during the day and roosted together at night. McCubbin (1971) refers to aggregations in sheltered gullies on Lindeman and Magnetic Islands and speculates that the species migrates to congretation sites in the winter months. In April, 1981, great numbers accumulated around lighthouses at Sandy Cape, on Fraser Island, and at Bustard Head during a migration (P. Sutton, pers. comm.). More than 10 discrete aggregations of this species were noted on South Percy Island on November 14, 1981 (G. Rces, pers. comm.), each having a proportion of specimens in active flight during daylight hours. Notwithstanding McCubbin's speculations, it seems that the aggregations of *Danaus hamata* are of a different nature to those described for *Euploea* spp. in that they never become completely quiescent and there are no records of long occupation of a single aggregation site. It seems best to regard them as temporary, topographically-induced concentrations of migrating populations. There are other Australian records of temporary migration-associated aggregations of Lepidoptera which also seem quite unrelated to the long term seasonal aggregations in tropical monsoon forests being described here, viz. *Anaphaeis java teutonia* (Fabricius) 1775 and *Catopsilia pyranthe crokera* (W.S. Macleay) 1826 in Sydney (Waterhouse & Lyell) 1914; *Pieris rapae* (Linn.) 1758 in Adelaide (McFarland, 1971); *Danaus chrysippus petilia* (Stoll) 1790 near Perth (Alexander, 1933); and *Alcides zodiaca* Butler in North Queensland (Coleman & Monteith, 1981 and references therein).

DISCUSSION

The dry-season aggregation behaviour described in this paper appears to be a specialized phenomenon of the mosoon zone of Australia, all localities mentioned lying within the northern band where the influence of the monsoonal dry season is most marked. In this respect it is notable that there are no records of aggregations from the Cairns region (Mossman to Ingham), a climatic enclave within the monsoon zone where the winter dry season is dispelled by orographic rain systems. This is despite the fact that all species of Hemiptera and Lepidoptera discussed occur there. The Cairns region is heavily populated and much frequented by naturalists so it is unlikely that aggregating insects there would go unnoticed.

Long-term aggregations of insects south of the monsoon zone in Australia are the exception but include summer congregations of Bogong Moths *(Agrotis infusa* (Boisd.)) on summits of the Australian Alps (Common, 1954) and winter roosts of the introduced Monarch butterfly, *Danaus plexippus* (Linneaus) in southern Australia (Smithers, 1965). The latter butterfly's behaviour in Australia is an incipient version of its well-documented migration-aestivation behaviour in its native North America (Urquhart, 1960).

While short-term communal roosting of butterflies, either during migrations as mentioned earlier, or as a regular nocturnal habit of certain species, e.g. South American heliconiines (Poulton, 1931; Benson & Emmel, 1973), is a frequent occurrence in the tropics, there are few recorded parallels overseas of the long-term aggregations of Australian *Euploea* spp. An exception is the study of the nymphalid, *Smyrna karwinskii* (Geyer) by Muyshondt & Muyshondt (1974) in El Salvador. This species migrates from lowlands to highlands during the dry season and forms small compact clusters of up to 100 individuals which remain quiescent for up to six months. The great numbers of individuals in the clusters of *Euploea core* in Australia seem unique among tropical butterflies.

The association of this aggregation behaviour with the dry season in tropical Australia is also clear, all records summarized being referable to the period from April to November. The only exception to this is Alexander's (1933) note on the aggregation of *Euploea core* at Westwood which he reports as being present at most times of the year during his 3 year's residence there.

The propensity of the insects for monsoon forest as their aggregation site is strong. The attractive feature of monsoon forest appears to be the cool, shady microclimate it affords. In the absence of monsoon forest other localized sites which offer a similar deep shade are selected. These include gorges, rock faces and groups of shady trees, particulary adjacent to water.

Although actual observations of migratory movements are lacking for the species concerned, it seems clear that for at least some species there is movement of populations from their normal open forest habitat into the monsoon forest patches at the end of the wet season for the purpose of forming aggregations. Those species for which we know sufficient of their normal habitat to be able to assume that such migration takes place include the bugs, *Lampromicra senator, Leptocorisa acuta, Noliphus erythrocephalus, Gralliclava*

australiensis and the butterfly *Euploea core corinna*. The same assumption of seasonal, inter-habitat migration can be made for certain non-aggregating species of insects also. In the Northern Territory the eminently 'open forest' butterflies, *Acraea andromacha, Danaus chrysippus* and *Junonia orithya* may be found inside monsoon forest at the height of the dry season (pers. obs.). A.L. Dyce and H.A. Standfast (pers. comm.) report that in the same region there is a contraction of populations of open forest frequenting mosquitoes (Culicidae) and biting midges (Ceratopogonidae) into the monsoon forest patches during the dry season. Similar dry season habitat changes are seen in certain bird species (Kikkawa et al., in press). Such habitat shifts are significant in the Australian context where there is generally a very basic difference in the biota inhabiting closed forests and open habitats. Within the monsoon zone the importance of the small areas of closed canopy monsoon forest as seasonal refugia for the fauna of the whole region is highlighted.

The function of the aggregating behaviour itself appears to be one of group reinforcement of the natural defences of the individual insects. All the Hemiptera and Lepidoptera species concerned have chemical defences against predation in the form of either toxic body fluids derived from toxic food plants (the butterflies) or volatile, repugnatorial secretions emitted from metapleural scent glands (the Hemiptera). Clearly these defensive powers are magnified in the aggregations. The massed flight behaviour of the aggregations when disturbed also has an apparently defensive function. The swirling, chain reaction of massed flight seen in roosting areas of *Euploea* species is quite spectacular and could be assumed to be confusing and alarming to a potential predator. In the Hemiptera where sudden massed flights were elicited by disturbance of aggregations (*Leptocorisa acuta* and *Coptosoma lyncea*) flight was accompanied not only by discharge of the repugnatorial glands but also by sudden loud buzzing similar to that of a disturbed paper-wasp nest. This combination of factors yielded considerable fright reaction, even in humans coming suddenly on an aggregation. For the aggregating Diptera observed, the group defence function of the behaviour is not so obvious. The exception is the sudden high-pitched buzzing of disturbed clusters of the milichiid species which also gave a wasp-nest fright response in humans.

LITERATURE CITED

ALEXANDER, W.B., (1933). Australian danaine, euploeine and pierine butterflies and uraniid moths. *In* E.B. Poulton. The gregarious resting habits of danaine butterflies in Australia; also of heliconine and ithomiine butterflies in tropical America. *Proc. Roy Ent. Soc. London* **7** (3): 64-5.

ANONYMOUS, (1974). Map: Isla Gorge Nat. Park – points of interest – QNC Camp 18–25 August, 1973. *Qd Nat.* **21**: 101.

BAILEY, W.J. and K.T. RICHARDS. (1975). A report on the insect fauna of the Prince Regent River Reserve, North West Kimberley, Western Australia. *In* J.M. Miles & A.A. Burbidge, (Eds), A biological survey of the Prince Regent River Reserve, North West Kimberley, Western Australia. *Wildl. Res. Bull. West. Aust.* **3**: 1–116.

BANKS, J., (1962). 'The *Endeavour* Journal of Joseph Banks 1768–1771.' Ed. J.C. Beaglehole. 2 Vols. Pub. Lib. NSW and Angus & Robertson, Sydney.

BENSON, W.H. and T.C. EMMEL (1973). Demography of gregariously roosting populations of the nymphaline butterfly *Marpesia berania* in Costa Rica. *Ecology* **54** (2): 326–35.

BREEDEN, S. & K., (1975). 'Australia's North — A Natural History of Australia.' Vol. 3. Collins, Sydney. 208pp.

COLEMAN, N.C. and G.B. MONTEITH, (1981). The life history of the North Queensland day-flying moth, *Alcides zodiaca* Butler (Lepidoptera: Uraniidae). *N. Qd Nat.* **45**(179): 2–6.
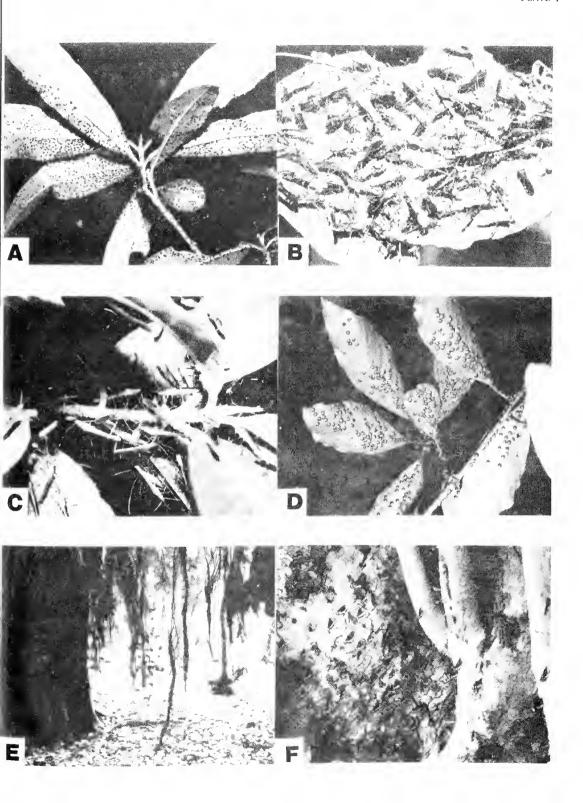
COMMON, I.F.B., (1954). A study of the ecology of the adult Bogong Moth, *Agrotis infusa* (Boisd.) (Lepidoptera : Noctuidae), with special reference to its behaviour during migration and aestivation. *Aust. J. Zool.* **2**: 221–63.

CSIRO DIVISION OF ENTOMOLOGY, (1975). 'Alligator Rivers Region Environmental Fact-Finding Study, Entomology.' Unpublished report.

DOLLING, W.R., (1978). A revision of the Oriental pod bugs of the tribe Clavigrallini (Hemiptera: Coreidae). *Bull. Brit. Mus. (Nat. Hist).* **36**(6): 281–321.

FERRAR, P., (1978). Macrolarviparous reproduction in *Euphumosia* (Diptera : Calliphoridae). *J. Aust. Ent. Soc.* **17**: 13–7.

KERSHAW, J.A., (1915). 'A naturalist in Northern Queensland.' Part 2. *Vict. Nat.* **31**: 161–72.

KIKKAWA, J. and G.B., MONTEITH, (1980). 'Animal Ecology of Monsoon Forests of the Kakadu Region. Northern Territory.' 116pp., Unpubl. report to the Australian National Parks and Wildlife Service.

KIKKAWA, J., L.J. WEBB, M.B., DALE, G.B. MONTEITH, J.G. TRACEY and W.T. WILLIAMS, (in press). Gradients and boundaries of monsoon forests in Australia. *Proc. Ecol. Soc. Aust.*

KING, P.P., (1826). 'Narrative of a Survey of the Intertropical and Western Coasts of Australia Performed Between the Years 1818 and 1822.' 2 Vols. John Murray, London.

LE SOUEF, J.C., (1971). Winter insect collecting in the Northern Territory. *Vict. Nat.* **88**: 350–6.

McCUBBIN, C.W., (1971). 'Australian Butterflies.' Nelson, Melbourne. 206pp.

McDONALD, F.J.D., (1963). Nymphal systematics and life histories of some Queensland Scutellerinae Leach (Hemiptera: Pentatomidae). *Pap. Dept. Ent. Univ. Qd* **1**(17): 277–95.

McFARLAND, A.N., (1971). A specialized case of communal roosting in *Pieris rapae. J. Lepid. Soc.* **25**(2): 144–5.

McNEIL, F.A., (1937). Notes on the gregarious resting habit of the danaine butterfly, *Danaus melissa hamata* W.S. Macleay, in the Whitsunday Islands of the east coast of Queensland *Proc. Roy. Ent. Soc. London* **12**: 108.

MONTEITH, G.B., (1972). Dry season insect aggregations in the Gulf Country. *News. Bull. Ent. Soc. Qd* **87**: 13.

MUYSHONDT, A. and A. MUYSHONDT, Jr., (1974). Gregarious seasonal roosting of *Smyrna karwinskii* adults in El Salvador (Nymphalidae). *J. Lep. Soc.* **28**: 224–9.

POULTON, E.B., (1931). The gregarious sleeping habit of *Heliconius charitonia* L. *Proc. Roy. Ent. Soc. London* **6**: 71.

SANDS, D.P.A., (1978). The biology and ecology of *Leptocorisa* (Hemiptera:Alydidae) in Papua New Guinea. *Res. Bull.* **18**, Dept. Primary Industries, Port Moresby.

SMITHERS, C.N., (1965). A note on overwintering in *Danaus plexippus* (Linnaeus) (Lepidoptera, Nymphalidae) in Australia. *Aust. Zool.* **13**(2): 135–6.

URQUHART, F.A., (1960). 'The Monarch Butterfly.' University of Toronto Press, Toronto. 261pp.

WATERHOUSE, G.A., (1932). 'What Butterfly is That?' Angus & Robertson, Sydney. 291pp.

WATERHOUSE, G.A. and G. LYELL, (1914). 'The Butterflies of Australia. A Monograph of the Australian Rhopalocera.' Angus & Robertson, Sydney. 239pp.

WEBB, L.J., (1978). A general classification of Australian rainforests. *Aust. Plants* **9**: 349–63.

PLATE 1
A. Aggregating flies of the family Milichiidae on foliage near Mount Gilruth, Northern Territory, July 1979.
B. A pure cluster of the alydid bug, *Noliphus erythrocephalus,* on foliage at the Stewart River, Cape York Peninsula, June 1976.
C. *Leptocorisa acuta,* clustering of foliage at Kemp Airstrip, Northern Territory, July 1979.
D. Quiescent aggregation of the plataspid bug, *Coptosoma lyncea* on foliage at Cahill's Crossing, Northern Territory in July 1979.
E. *Euploea core* and *E. sylvester* resting on aerial roots of *Ficus virens* at North Point, Northern Territory, July 1979.
F. *Euploea core* and *E. sylvester* resting on trunk of *Ficus virens* at North Point, Northern Territory, July 1979.

SAURICHTHYS (PISCES, ACTINOPTERYGII) FROM THE EARLY TRIASSIC OF QUEENSLAND

SUSAN TURNER
Queensland Museum

ABSTRACT

The first description of a Triassic fish from Queensland is based on part of a skull of *Saurichthys* cf. *S. gigas* (Woodward 1890) from the freshwater Arcadia Formation at Rewan Crater, SE Queensland. Its occurrence confirms the age of the Rewan vertebrate fauna as no older than Lower Triassic.

INTRODUCTION

The Triassic fishes of Queensland are virtually unknown. Hills (1958) mentioned the existence of fragmentary (though unspecified) fish remains, and the rich vertebrate fauna of the Arcadia Formation (formerly the Rewan Formation, see Jensen 1975) is known to include patches of actinopterygian scales preserved in coprolites, and occasional lungfish toothplates (Bartholomai and Howie 1970, Howie 1972). The first identifiable portion of fish skull was recently collected from the Arcadia Formation and is described here. The skull fragment is referred to the cosmopolitan Triassic genus *Saurichthys,* and its discovery supports dating of the Arcadia fauna as Early Triassic rather than Late Permian (see discussion by Warren 1980).

SYSTEMATICS

Class OSTEICHTHYES
Subclass ACTINOPTERYGII
Order SAURICHTHYIFORMES
Family SAURICHTHYIDAE Goodrich 1909
Genus *Saurichthys* Agassiz 1834
Type Species *Saurichthys apicalis* Agassiz 1834
Saurichthys cf. *S. gigas* (Woodward 1890) =
Belonorhynchus

MATERIAL: Single portion of skull between the posterior part of the orbitotemporal region and the anterior part of the labyrinthian region, covered by ornamented dorsal and lateral bones, and the corresponding mandibles. Queensland Museum specimen — QMF11942 (Pl. 1).
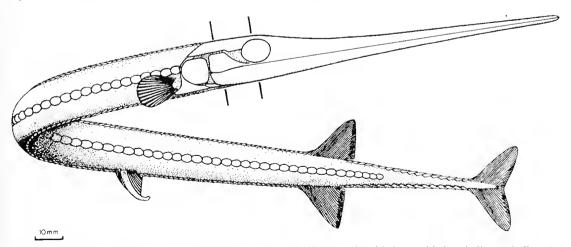
FIG. 1. Reconstruction of *Saurichthys calcaratus* (from Griffith 1977), with bars added to indicate skull region preserved in the Queensland *Saurichthys,* QMF11942.

LOCALITY: The Crater, on Rewan property, about 72 km southwest of Rolleston, SE Queensland (QM field locality L78). This locality, a steep-walled basin, has been described by Howie (1972) and by Thulborn (1979). The specimen was found lying loose in a gully on the western flank of the Crater.

HORIZON: Middle part of the Arcadia Formation, Rewan Group; Lower Triassic.

DESCRIPTION

The specimen represents the posterior part of the orbitotemporal region to the anterior otic region of an uncrushed, virtually undistorted skull, with corresponding dermal bones and mandibles in place. It is 29 mm long, a little deeper than wide (21 mm by 16 mm), and tapers slightly to the front. This fossil is almost rectangular in cross-section, with a flat roof and near-vertical sides, and is filled with dark brown ferruginous sandstone (see Fig. 2). The dermal bones are thin and rather fragile and in some places have been stripped away by weathering, making it difficult to trace sutures with certainty. A thin coating of ferruginous sand which covered the specimen, especially between mandibles and maxillae, has been removed with a fine needle.

Comparison with other *Saurichthys*, e.g. *S. ornatus* (Stensiö 1925) and *S. madagascariensis* (Beltan 1968, Rieppel 1980), indicates that the preserved area of the skull roof is probably formed by frontal, parietal and 'dermopterotic' (dermopterotic-extrascapular) bones (Pl. 1 A1, 2). In this specimen these bones are not demarcated by sutures, but their general relationships are indicated by variations in the ornament of the skull roof. Between the orbits (region of frontals) this ornament consists of small circular and elliptical tubercles without preferred orientation; behind the frontal region in the middle of the skull roof (region of parietals) is a whorl of elongate tubercles arranged concentrically; the greater part of the posterior and lateral dermal roof is occupied by 'dermopterotics' where the ornament consists of elongate tubercles aligned longitudinally.

The 'dermopterotic' bones curve down onto the sides of the skull. Part of the anterior portion of the left side is depressed with a small elliptical hole through it (Pl. 1 A1, 2, 'pw'). This may represent a part of the fossa Bridgei which extends on the dorsal face of the otic region (cf. Stensiö 1925), or alternatively, as it is still surrounded by ornamented bone, it may be a puncture wound. The 'dermopterotics' are separated from the bones of the cheek region by a definite gap, which forms

a distinct groove on the left posterolateral side. The lower margin of the 'dermopterotic' above the orbit forms a slight overhang marked by a distinct notch.

Much of the cheek region is formed by a large triangular combined maxilla-preopercular (Pl. 1 B1, 2) with its ornament of fine and closely spaced striae trending down and slightly forwards so characteristic of the genus *Saurichthys*. The maxilla curves anteriorly to correspond to the posterior edge of the orbit and tapers to a slender process below the large space which would have accommodated the eye. The striae curve anteriorly to run parallel with the ventral edge of the maxilla. Scleral ossicles, supraorbitals and infraorbitals, which delimit the orbit in *Saurichthys* species, are not present in the specimen, as in *S. calcaratus* Griffith 1977. The ventral edge of the maxilla-preopercular is roughly horizontal, but extends downwards at the back to form a slight overlap on the mandible. The preopercular is poorly preserved and the suture line with the maxilla is not clear. The dermal ornament is weathered leaving an irregular line across the combined bones (Pl. 1 B2).

The robust mandible is elliptical in cross-section and accounts for some 40% of the total skull depth. It consists mainly of dentalosplenial and the ornament of near vertical striae is preserved on its upper half. No teeth are visible in the specimen, but this is not surprising since teeth of *Saurichthys*, where present, are often confined to the preorbital region of the skull and mandibles (see e.g. *S. nepalensis* Beltan & Janivier 1978; *S. obrutchevi* described by Minich 1981).

DISCUSSION

REMARKS ON RELATIONSHIPS

In its shape, its proportions, and the arrangement of its skull bones the specimen agrees closely with the equivalent regions of other *Saurichthys* skulls (see review by Beltan & Tintori 1980). The specimen shares the following distinctive features with other species of *Saurichthys*: the box-like shape of the skull with relatively narrow roof and deep flat sides; the combined maxilla-preopercular and exceptionally deep mandible with the ornament of striae; the skull roofing bones are demarcated not by sutures but by ornament.

There are six other reports of *Saurichthys* from the Triassic of Australia:

Saurichthys gigas (Woodward 1890) (*Belonorhynchus*), from the Narrabeen Group (Lower Triassic) of Gosford, NSW, and Hawkesbury Sandstone of Somersby Falls, NSW (Ritchie 1981);

Saurichthys gracilis (Woodward 1890) (*Belonorhynchus*), from the Narrabeen Group of Gosford, erroneously referred to as *B. elegans* by Wade (1940);

Saurichthys parvidens Wade 1935, from the Hawkesbury Sandstone (Middle Triassic) of Brookvale, NSW;

Saurichthys sp. from the Knocklofty Formation (Lower Triassic) of SE Tasmania (Banks *et al.* 1979);

Saurichthys sp. from the Blina Shale (Lower Triassic) of the Erskine Range, Western Australia (Warren 1980).

A specimen from Gosford, NSW, supposedly a saurichthyid, was figured by Eastman (1917, p. 281, pl. 14, fig. 3) who suggested it was an 'aberrant' form. More likely it is not a saurichthyid at all as it exhibits none of the features common to the family.

Only *Saurichthys gigas* and *S. gracilis* have been described in any detail (Woodward 1890); these two species differ principally in size and body proportions, the head with opercular apparatus occupying about one-third total length in *S. gigas* and about one-quarter in *S. gracilis*.

Both of these forms have fine striations on maxillae and mandibles, but these striations have an irregular pattern in the hind portion of the mandibular of *S. gigas* and are oriented longitudinally, curving upwards behind in that of *S. gracilis*. In the Queensland specimen the posterior part of the jaws is missing and, consequently, the pattern is unknown. In *S. gigas* the skull roofing bones carry 'delicate ridges or striations' which are 'somewhat irregular and confused' (Woodward 1890, p. 24). Overall, the Queensland specimen is comparable to *S. gigas* in its basic structure and in the pattern of its dermal ornament. It seems to show fewer resemblances, except perhaps for size, to *S. gracilis*, which Woodward stated was of 'more delicate proportions'. In view of the similarities the Queensland specimen is provisionally designated *Saurichthys* sp., cf. *S. gigas*.

Most species of *Saurichthys*, including the Gosford specimens, have four longitudinal rows of scutes, often large ones (see Fig. 1). Rieppel (1980), however, has described a *Saurichthys madagascariensis* with a very well-preserved complete squamation. The patches of small actinopterygian scales reported from the Arcadia Formation do not appear to be like those described but it is possible that some scales may belong to very young *Saurichthys*.
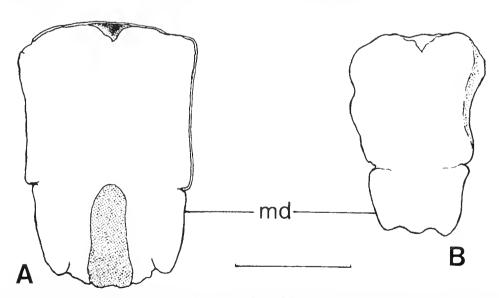
FIG. 2. *Saurichthys* cf. *S. gigas*. Diagrammatic cross-sections of QMF11942. A, ventral view showing thin dermal bones. At the midpoint of the dorsal edge is a v-shaped notch lined with endocranial bone. Between the mandibles is a plug of fine-grained pink sediment (stippled) otherwise the specimen is infilled with sandstone. B, dorsal view. Bar = 1 cm, md = mandible.

The genus *Saurichthys* is sometimes regarded as 'subholostean' (Romer 1966) and has been placed among the chondrostean fishes (Gardiner 1967). The relationship to other groups of bony fishes is uncertain and seems to be between the Palaeoniscidae and the sturgeons.

PALAEOECOLOGY

Saurichthys species were slim, long-bodied fishes resembling modern pike, *Esox,* and gar-pike, *Lepisosteus,* in general appearance, but possibly more like the recent *Belone,* an excellent swimming fish, in life-style with its fusiform body and rostrum resulting from the elongation of the ethmoidal region. The narrow box-like skull extended forwards as a long tapering beak armed with sharp conical teeth, in some cases representing up to one-third body length (see Fig. 1). *Saurichthys* species with reduced squamation also resemble living sturgeons (Acipenseriformes).

Saurichthys parvidens reached a length of at least 75 cm (Wade 1935), whereas Woodward (1890) estimated that *S. gigas* and *S. gracilis* attained at least 49 cm and 28 cm respectively. A recently found specimen of *S. gigas* was 70 cm long and Ritchie (1981) estimated a total length of 105 cm. On the basis of skull measurements it is estimated that the Rewan *Saurichthys* specimen had a body length of 28 to 32 cm.

Most *Saurichthys* species have been described as marine fishes (e.g. Berg 1958), though some, including the Australian forms, have been found in non-marine environments. Beltan and Tintori (1981) reviewed the distribution of *Saurichthys* and concluded that the genus was adapted to both marine and fresh waters. These authors mentioned the possibility that *Saurichthys* might have been a potamodromous fish which might swim up river to spawn. The Australian species have all been found in sediments interpreted as freshwater (see David (1890) and Ritchie (1981) on NSW environments; Banks *et al.* (1979) on Knocklofty and Blina Shale environments; Bartholomai (1979), Thulborn (1979) and Warren (1972, 1980) on the Arcadia environment), and may well have been restricted to freshwater, like the North American sturgeons, or anadromous and euryhaline, like the European sturgeons. In any event *Saurichthys* probably would have been an active predator on smaller fishes and tetrapods.

AGE

The genus *Saurichthys* occurs worldwide in the Triassic: in Canada, Greenland, Spitsbergen, throughout Europe, and in the U.S.S.R., Turkey, Nepal, South Africa, Malagasy, and Australia (Beltan and Tintori 1981, Minich 1981). The genus first appears in the Early Triassic (Induan, Andrews *et al.* 1967; Eotriassic, Beltan and Tintori 1981). Consequently the presence of *Saurichthys* in the Arcadia Formation would seem to confirm that the associated fauna is Triassic, rather than Late Permian (cf. Warren 1980). Furthermore by comparison with other *Saurichthys* from Australia the dating would be Lower to Middle Triassic.

ACKNOWLEDGEMENTS

LITERATURE CITED

AGASSIZ, L., 1834. Aberissene Bemerkungen über fossile Fische. *N. Jb. Mineral., Geol. Paläont.* **1834**: 379–90.

ANDREWS, S.M., B.G. GARDINER, R.S. MILES, and C. PATTERSON, 1967. Pisces. In 'The Fossil Record'. (London: Geol. Soc. Lond.) 637–83.

BANKS, M.R., J.W. COSGRIFF, and N.R. KEMP, 1979. A Tasmanian Triassic Stream Community. *Aust. Nat. Hist.* **19**(5): 150–7.

BARTHOLOMAI, A., 1979. New Lizard-like reptiles from the Early Triassic of Queensland. *Alcheringa,* **3**: 225–34.

and A. HOWIE, 1970. Vertebrate Fauna from the Lower Triassic of Australia. *Nature* **225** (5237): 1063.

BELTAN, L., 1968. La faune ichthyologique de l'Eotrias du NW de Madagascar: la neurocrâne. *Cah. Paléont.* (CNRS) **1968**: 1–135.

and P. JANVIER, 1978. Un nouveau Saurichthyidae (Pisces, Actinopterygii) *Saurichthys nepalensis* n. sp. du Trias inférieur des Annapurnas (Thakkhola, Népal) et sa signification paléobiogéographique. *Cybium* 3e ser., **4**: 17–28.

and A. TINTORI, 1981. The genus *Saurichthys* (Pisces, Actinopterygii) during the Gondwana Period. In M.M. Creswell and P. Vella (eds.), 'Gondwana Five', (Rotterdam: A.A. Balkema) p. 53–9.

BERG, L.S., 1958. 'System der Rezenten und Fossilen Fischartigen und Fische'. (Berlin: Deutscher Verlag der Wissenschaften) i–xi, 1–310.

DAVID, T.W.E., 1890. Stratigraphical note on the fish-bed at the Railway Ballast Quarry near Gosford. *Mem. Geol. Surv. NSW, Palaeont.* **4**: vii–xi.

EASTMAN, C.R., 1917. Fossil Fishes in the Collection of the United States National Museum. *Proc. U.S. Nat. Mus.* **52**: 235–304.

GARDINER, B.G., 1967. Further notes on Palaeoniscoid fishes with a classification of the Chondrostei. *Bull. Brit. Mus. (Nat. Hist.) Geol.* **14**, 5: 145–206.

GRIFFITH, J., 1977. The Upper Triassic fishes from Polzberg bei Lunz, Austria. *Zool. J. Linn. Soc.*, **60**: 1–93.

HILLS, E.S., 1958. A Brief Review of Australian Fossil Vertebrates. In 'Studies on Fossil Vertebrates', Ed. T.S. Westoll (London: The Athlone Press, Univ. London) 86–107.

HOWIE, A.A., 1972. On a Queensland labyrinthodont. In 'Studies in Vertebrate Evolution', Eds K.A. Joysey and T.S. Kemp. (Edinburgh: Oliver & Boyd) 50–64.

JENSEN, A.R., 1975. Permo-Triassic stratigraphy and sedimentation in the Bowen Basin, Queensland. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* **154**: viii + 187 p.

MINICH, A.V., 1981. Zaoorichtis iz Triasa SSSR. *Paleont. Zhur.* **1981** (1): 105–13 (in Russian).

RIEPPEL, O., 1980. Additional specimens of *Saurichthys madagascariensis* Piveteau, from the Eotrias of Madagascar. *N. Jb. Geol. Paläont. Mh.* **1980**, 1: 43–51.

RITCHIE, A., 1981. First complete specimen of the dipnoan *Gosfordia truncata* Woodward from the Triassic of New South Wales. *Rec. Austr. Mus.* **33**, 11: 606–16.

ROMER, A.S., 1966. 'Vertebrate Paleontology', (Chicago & London: The University of Chicago Press) 1–468.

STENSIÖ, E.A., 1925. Triassic fishes from Spitzbergen, Part II. *Kungl. Svensk. vetensakad. handl.*, Ser. 3, **2**, 1: 1–261.

THULBORN, R.A., 1979. A proterosuchian thecodont from the Rewan Formation of Queensland. *Mem. Qd Mus.* **19** (3): 331–55.

WADE, R.T., 1935. 'The Triassic Fishes of Brookvale, New South Wales', (London: British Museum (Nat. Hist.)) i–xiv, 1–89.

1940. The Triassic Fishes of Gosford, New South Wales. *J. Proc. Roy. Soc. NSW,* **73**: 206–17.

WARREN, A., 1972. Triassic amphibians and reptiles of Australia in relation to Gondwanaland. *Aust. Nat. Hist.* **1972**: 279–83.

1980. *Parotosuchus* from the Early Triassic of Queensland and Western Australia. *Alcheringa* **4**: 25–36.

WOODWARD, A.S., 1890. The Fossil Fishes of the Hawkesbury Series at Gosford. *Mem. Geol. Surv. NSW, Palaeont.* **4**: 1–55.

NOTE ADDED IN PROOF

The folowing reference came to my attention too late to be included in the discussion:

DZIEWA, T.J., 1980. Early Triassic osteichthyans from the Knocklofty Formation of Tasmania. *Pap. Proc. Roy. Soc. Tasmania,* **114**: 145–60.

This mentions *Saurichthys* sp. from Coningham, Tasmania (pl. 7, 8,).

PLATE 1.
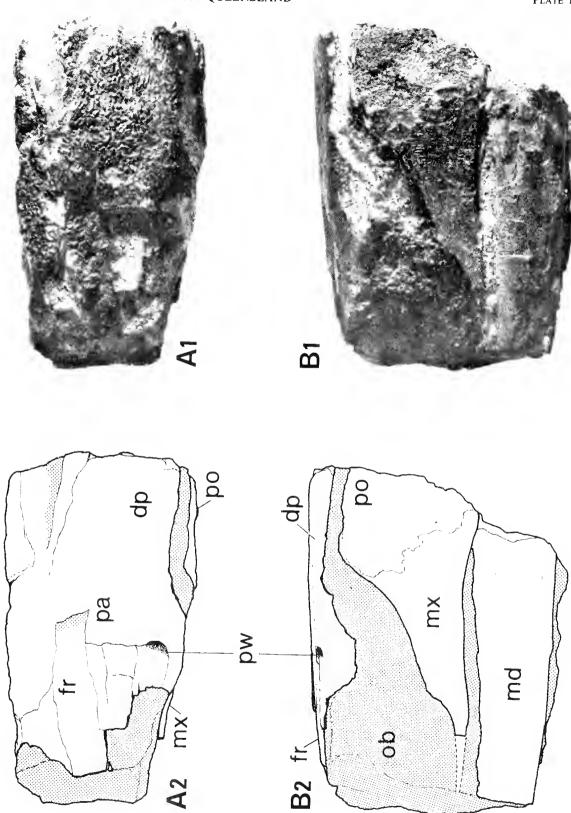
SAURICHTHYS cf. *S. GIGAS* (WOODWARD, 1890), QMF11942.

FIG. A1. Dorsal view of skull roof showing dermal ornament. Note central whorl of tubercles in parietal area, and lack of obvious sutures.

FIG. A2. Interpretation of A1, with depressed fractures in the frontal region. Abbreviations below.

FIG. B1. Left lateral view of skull showing dermal ornament of striations on the mandible and maxilla. Anterior is toward the region of the orbit filled with matrix.

FIG. B2. Interpretation of B1.

Legend: dp — 'dermopterotic', fr — frontal, md — mandible, mx — maxilla, ob — orbit, po — preopercular, pw — hole in dermal roof, possibly a puncture wound, or alternatively the anterior fossa Bridgei.

Stipple denotes matrix. All x 3.

THE EMBRYOLOGICAL DEVELOPMENT
OF THE QUEENSLAND LUNGFISH,
NEOCERATODUS FORSTERI, (KREFFT)

A. KEMP

Queensland Museum

ABSTRACT

The development of *Neoceratodus forsteri* is described for a comparison with development of *Lepidosiren paradoxa* and *Protopterus annectens* (Kerr 1909) and for a revision of Semon's (1893) studies on *N. forsteri*. Fertilised eggs of *N. forsteri* are hemispherical, 3–3·5 mm in diameter, telolecithal and green or brown in colour, with dark pigment granules in the cortex. The first three cleavages are usually meridional, followed by a latitudinal cleavage and then by increasingly irregular and asynchronous divisions. The dorsal lip of the blastopore is initially an irregular curved slit, but develops into a smooth crescentic shape. The lateral lips draw close together before a ventral lip forms. The blastopore of the early neurula is a dorsoventrally orientated slit which develops into an oval anus connected with the nervous system by the neurenteric canal until stage 34. Primary brain divisions and optic vesicles are present before the neural folds close. The neural rudiment forms as a tube and always retains this structure.

Morphogenesis of the nares is closely linked to the development of the upper lip. The lateral line system of the trunk first appears at stage 41 and at stage 43–44 on the head. By stage 45 the main lines of the head are visible and by stage 47, all lines have developed into a series of pits. The pronephros shows externally from stage 27 until 35 and is a useful guide to development between these stages. Until stage 31, the endoderm cell mass retains its globular shape while the head grows forwards, but this shape is progressively lost after stage 32 when the body axis lengthens and the tail bud grows. At stage 37–38 endodermal cells still laden with yolk globules are packed together in platelet fashion. The amount of yolk is noticeably reduced by stage 43, although a little is still present at stage 47 when the spiral valve becomes visible. Yolk has entirely disappeared by stage 49.

Pectoral fins appear at stage 42 in lake fish (44 in river fish) and become pigmented at stage 43. Fin skeletons are visible at stage 47. Pelvic fins follow a similar course of development but appear later, at stage 48 in lake fish, and at stage 50 in river fish. Dorsal and ventral medial fins start to develop at stage 35 when the axis of the body begins to extend. The dorsal fin extends as far fowards as the back of the head at stage 38 and then regresses so that it reaches only as far as the middle of the trunk at stage 54. A large pre-anal ventral fin, which never develops a skeleton, is present from stages 40–53, reaches a peak at stage 49 and is then resorbed. Scales do not appear until stage 52, and are well established by stage 54. Melanin appears at stage 36 under the epidermis, and melanophores are widespread by stage 42. Cells containing a red pigment are present at stage 43.

There is no obvious metamorphosis. The adult form develops gradually over a period of months.

INTRODUCTION

The Queensland lungfish, *Neoceratodus forsteri* (Krefft) was regarded as a giant amphibian when it was first discovered (Krefft, 1870). Though it was soon clear that it was a fish, (Günther, 1871) its embryonic development closely resembles that of the Urodela.

Semon (1893) described the external develop- ment of *N. forsteri,* based on observations of eggs and larvae. In the present study a comparison of eggs and embryos collected in successive seasons and observation on living specimens as they developed have added new information. For this reason a revised version of the external development of *N. forsteri* is presented which differs in some details from that of Semon (1893).
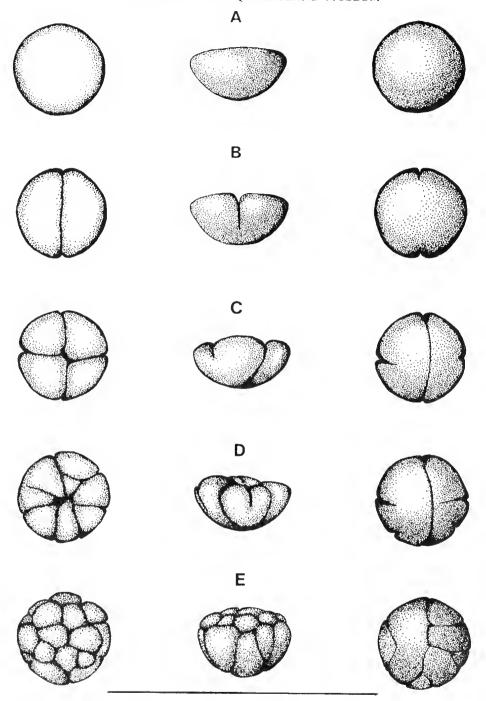
FIG. 1. Normal series of divisions in early cleavage in *Neoceratodus forsteri* eggs, stages 1-5, drawn with a camera lucida from fixed specimens removed from the vitelline and albumen membranes. The flat surface is shown on the left, side view in the centre and the convex surface on the right. A, stage 1, uncleaved egg; B, stage 2, first meridional cleavage; C, stage 3, second meridional cleavage at right angles to the first; D, stage 4, the third meridional cleavage, slightly irregular, with furrows on the convex surface lagging but usually dividing the cells from apex to base; E, stage 5 showing the first latitudinal cleavage, loss of the hemispherical shape as the segmentation cavity develops and delayed furrows in the convex surface. Scale line = 1 cm.

The stages of development given here for *N. forsteri* correspond closely to the stages described by Kerr (1909) for *Lepidosiren paradoxa* and *Protopterus annectens*.

MATERIALS AND METHODS

Eggs of *N. forsteri* were collected from Enoggera Reservoir, Brisbane, Queensland, (1969–1974) and from the Brisbane River over 3 seasons 1977–1979, and reared under the conditions described by Kemp (1981).

Most of the following description has been based on observations of living specimens as they developed, and of a series of fixed eggs, embryos and larvae. Living eggs were observed at frequent intervals during development at temperatures of 18°C, 20°C, and 22°C.

Embryos were removed from the membranes and fixed in 5% neutral buffered formalin. A series of fixed embryos from stages 20–39 were dehydrated in alcohol and cleared in cedar wood oil to show internal detail. The descriptions are based largely on eggs from Enoggera Reservoir and eggs from the River are described when they are different.

RESULTS

THE EGG

The egg is telolecithal, enclosed in a jelly capsule (outer albumen) about 2–3 mm thick. This is sticky when first laid, and allows the egg to adhere to water weeds. The external surface of the albumen soon becomes covered with debris and microscopic plant and animal life and the jelly loses its stickiness unless it is accidentally detached from the weed, when the freshly-exposed layer of albumen is adhesive again.

Within the outer albumen membrane there are two membranes, the inner albumen and the vitelline respectively. They are closely applied to each other but clear of the egg surface (Pl. 1A). The fluid filled space enclosed by the membranes is spherical and the diameter slightly larger than that of the egg itself (Pl. 1A).

The fertilised uncleaved egg from Enoggera Reservoir is hemispherical, 3–3.5 mm in diameter (Fig. 1A; Pl. 1A), and lies free in the space formed by the vitelline membrane with the flatter side uppermost and the convex surface down. The egg is very delicate and the cytoplasm yolk laden. Eggs may be green or brown in colour depending on the colour of the yolk granules. Some dark pigment is present in the cortex of the egg, either on the flat surface, or on the convex surface or divided between the two (Pl. 1C and 1J). A spot,

paler than the ground colour of the egg, lies within the pigmented area of a number of eggs (Pl. 1A, D and J). In some eggs an irregular dark area (not associated with the pigment patch) was also present (Pl. 1A).

River eggs are rounder than lake eggs but are otherwise similar.

CLEAVAGE

Cleavage in *N. forsteri* is so often irregular that it is difficult to describe a normal series. Figs. 1, and 3, and Pl. 1C–I illustrate the 'normal' sequence and Fig. 2 and Pl. 1J–L some common variations. Cleavage stages are summarised in Table 1.

Stages 2–6 inclusive are cleavage stages (Pl. 1D–F and Figs. 1B–E and 3A). First cleavage is meridional, usually dividing the egg into two equal parts, and normally appears first at the pigmented uppermost surface and passes to the opposite side (Fig. 1B). First cleavage divides the pigment and the pale spot if present, but the cleavage products do not necessarily get an equal share of either even if they are equal in size themselves. Sometimes the pale spot is not divided (Pl. 1J).

When first cleavage has been equal, the second cleavage furrow (stage 3) is also meridional and will normally appear at right angles to the first and pass from the flat pigmented surface to the rounded unpigmented surface (Fig. 1C). Each of the resulting cells has some pigment and usually a portion of the pale spot if originally present (Pl. 1D). The small dark area of some eggs (Pl. 1A) disappears.

The previously mentioned flat pigmented area may take on pronounced rounded contours in living eggs at this stage, though it remains uppermost in the intravitelline space. Presumably that part of the egg which contains the larger yolk granules is heavier and remains beneath, pressed against the vitelline membrane.

The third cleavage, also meridional, cuts each quarter of the egg down the middle usually radially but sometimes at right angles to this (stage 4, Fig. 1D and Pl. 1E). Pigment retains its original position on the egg surface but is now divided between a number of cells, often unevenly. The pale spot is difficult to distinguish.

The fourth cleavage (stage 5) is the first latitudinal one and usually produces eight micromeres and eight macromeres (Pl. 1F and Fig. 1E). The micromeres have most of the egg pigment and are uppermost in the intravitelline space. The egg is more rounded on top, owing to
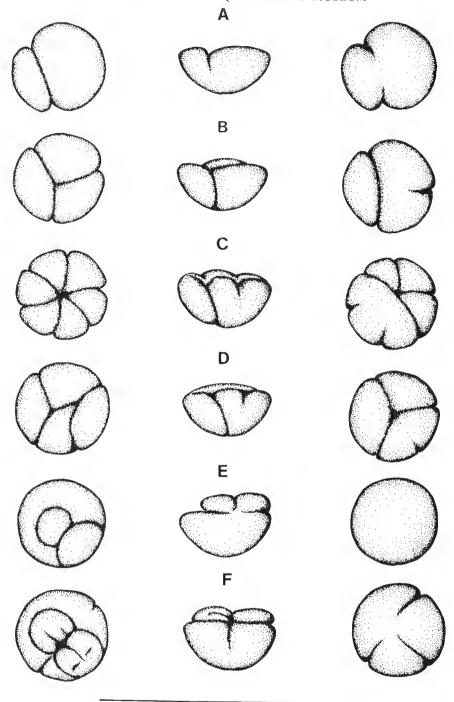
FIG. 2. Abnormal cleavages in a series of fixed eggs removed from the vitelline and albumen membranes before drawing. The flat surface is shown on the left, side view in the centre, and the convex surface on the right. A, common form of unequal first division; B, an egg divided into three equal cells; C, an egg with six equal cells; D, cleavage cf Semon's stage 5 (1893, table 1, fig. 50); E, an abnormal division resulting in a button of small cells on top of uncleaved yolky material; F, later cleavage of an egg of the type illustrated in Fig. 2E; the small cells have divided several times and a few cleavage furrows have appeared in the convex surface. Scale line = 1 cm.

A

B

C

D

E
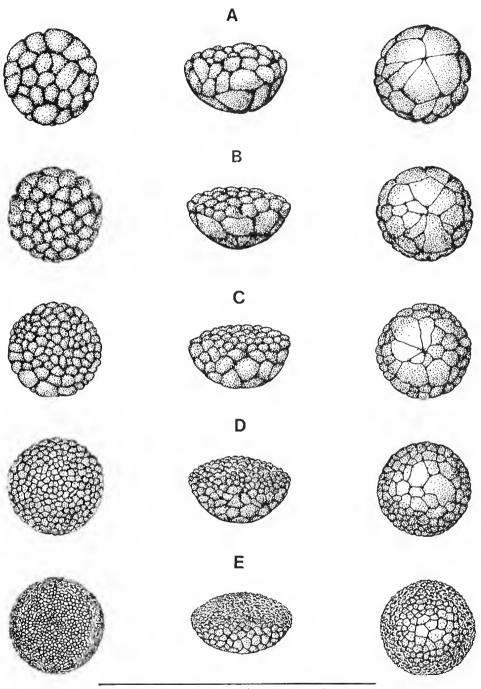
FIG. 3. Normal late cleavage stages and blastulae in *N. forsteri,* drawn from fixed specimens removed from the membranes. The flat surface is shown on the left, side view in the centre and convex surface on the right. A, stage 6, more horizontal and vertical cleavages; B, stage 7, cleavage continues more quickly among the smaller pigmented cells than in the heavily yolked cells of the convex surface; C, stage 8, large celled blastula; D, stage 9, a medium celled blastula; E, stage 10, a small celled blastula. The segmentation cavity (blastocoel) increases in size. Cells of the convex surface are flattened against the vitelline membrane (pavement cells), and the pigmented cells of the sides and roof of the blastocoel project into the intravitelline space and have rounded contours. Scale line = 1 cm.

the development of the segmentation cavity or blastocoel as space appears between the blastomeres. Cell division subsequently becomes asynchronous.

The fifth cleavage (stage 6) occurs quickly in the micromeres and is vertical. It is slower in the macromeres and here it tends to be latitudinal. The segmentation cavity increases in size (Fig. 3A).

Common variations of this pattern include gross disparity in the sizes of the cleavage products (Fig. 2A), and in the initiation of a cleavage furrow in the unpigmented rounded surface of a normally pigmented egg or in the pigmented rounded surface of an abnormally pigmented egg (Pl. 1J). Sometimes a latitudinal division occurs first (Fig. 2E).

If cleavage was unequal in the first division the smaller cell often divides first. A less frequent variation is the division of the larger cell to produce three cells of equal size (Fig. 2B), resulting in six equal sized cells instead of eight (Fig 2C). Several eggs cleaved unevenly in a manner reminiscent of Semon's stage 5, with two large cells flanking two smaller cells divided across the centre of the egg (Fig. 2D and Pl. 1K).

When first cleavage was latitudinal (Fig. 2E) the small cell on top of the uncleaved yolk continued to divide rapidly. The yolk mass lagged considerably (Pl. 1L and Fig. 2E and F).

FORMATION OF THE BLASTULA

The blastula forms during stages 7–11 (Figs. 3B-E, 4A; Pl. 1G, H, I; see Table 2). The cells continue to divide and the previously flat surface becomes more rounded as they project into the intravitelline space. Cells in the convex region are pressed against the membrane and resemble a pavement. Th segmentation cavity enlarges slowly until stage 11, when it expands rapidly to fill the entire intravitelline space. The cells of the thin walls and roof of the blastocoel are still rounded but those at the base are flattened against the vitelline membrane. The egg cannot rotate in the intravitelline space.

As the blastula develops it becomes clear that the position of the micromeres is correlated with the position of the egg pigment on the surface of the egg when it started to cleave, i.e. unusually placed pigment means unusually placed micromeres. This type of abnormality is smoothed over by stage 11 as cells move and a normal blastula is formed.

FORMATION OF THE GASTRULA

The gastrula forms during stages 12–16 (Figs. 4B–F, Pl. 2A, B). The earlier stages are prolonged (12, 13 and 14) but the process is completed quickly.

While gastrulation in *N. forsteri* usually follows the sequence of stages shown in Fig. 4, observations on living eggs reveal more variability e.g. an embryo in which formation of the anterior neural plate is advanced may also have a round yolk plug (7.5% of embryos). Such variation does not usually reduce the viability of the embryos — the yolk plug closes eventually and a normal neurula is formed. As with cleavage, 'abnormalities' are common and do not block development, unless they are extreme. The most common condition of gastrulation is described from a series of fixed embryos.

Between the small pigmented cells which cover the expanded blastocoel and the pavement cells of the base, an irregular slightly curved slit develops (Pl. 2A and Fig. 4B). Rounded cells have begun to invaginate and appear to be pulling in the pavement cells. The crescentic dorsal lip which develops from this slit (Fig. 4C) is more curved and smoother in outline. The pavement cells which have continued to divide take up less of the external area of the egg. At the outer limits of the crescent, rounded cells are being drawn inwards (Figs. 4C and D).

Next, the lateral lips form and draw together. Pavement cells are confined to the central area, under the dorsal lip, and more cells with pigment are involved in invagination (Fig. 4D). The lateral lips draw together but there is still no sign of a ventral lip except for a line of slightly indented cells where it would be expected to form (Fig. 4E). The external surface of the egg is entirely covered by pigmented cells and the pavement cells have disappeared. The blastocoel is smaller.

The ventral lip finally appears as a short section between the two lateral lips which have almost met in the midline (Pl. 2B and Fig. 4F). The blastopore is now slit-like dorsally where the lateral lips have met. The blastocoel is reduced in size, the egg is no longer spherical and there is sufficient space between the egg surface and the vitelline membrane for the embryo to rotate freely again. From the dorsal part of the blastopore runs a diffuse double streak of deeply pigmented cells which mark the position of the future neural plate. This part of the egg is also slightly flattened (Fig. 4F).

TABLE 1: CHARACTERISTICS OF STAGES 1–6.

Stage	External Features	Distribution of Pigment	Segmentation Cavity	Stage (Semon 1893)	Stages (Kerr 1909) L. paradoxa	P. annectens
1 (Fig. 1A; Plate 1A & C)	hemispherical, green or light brown in colour	irregular patch, on flat surface	—	—	—	—
2 (Fig. 1B)	hemispherical, first meridional furrow forms	irregular patch on flat surface of each cell	—	2	2	—
3 (Fig. 1C, Plate 1D)	hemispherical, second meridional furrow forms at right angles to first	shared roughly among the cells, on previously flat surface	—	4	3	—
4 (Fig. 1D, Plate 1E)	flat surface grows rounder; third meridional furrow bisects each cell	shared roughly among the cells, on previously flat surface	—	6	4	—
5 (Fig. 1E, Plate 1F)	egg more rounded, first latitudinal furrow appears	smaller cells have pigment, larger ones have none	small space in centre	7	—	—
6 (Fig. 3A)	flat surface furrows are vertical, convex horizontal; division no longer synchronous	pigment confined to micromeres	larger central space	9	7	VII
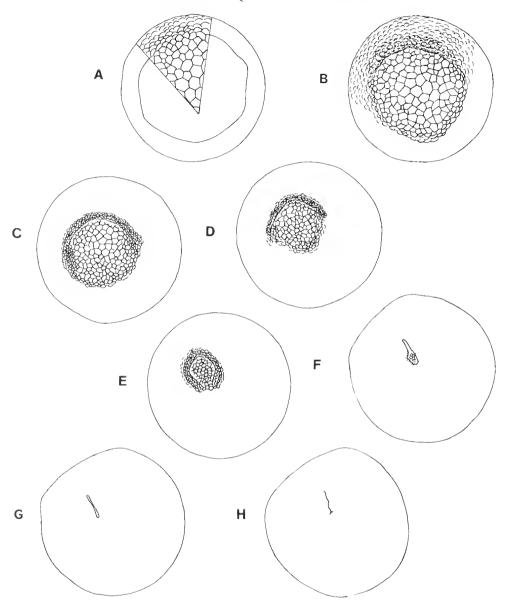
FIG. 4. Formation of the gastrula in *N. forsteri*. A series of fixed eggs drawn without removal from the membranes, because the blastocoel is now so large that it fills the entire intravitelline space and the egg cannot be removed without damage. All are views of the blastopore region and show details of the behaviour of the pavement cells and of the pigmented cells enclosing the blastocoel cavity. A, stage 11, showing the gradation from the pavement cells at the base of the egg to the cells at the sides of the blastocoel cavity which are smaller and rounder in shape. The solid line represents the limit of the pavement cells; B, stage 12, with an irregular slit shaped blastopore at the junction of the pavement and the pigmented cells. Cell division has continued and invagination involves pigmented cells rolling over the pavement cells; C, with a crescent shaped blastopore and invagination at the lateral lips as well as at the dorsal lip. The pavement cells are smaller and fewer in number; D, stage 14, with well formed lateral lips drawing closer together giving the blastopore the appearance of a wide V. Most of the pavement cells have been drawn inside; E, stage 15, still without a ventral lip, and with lateral lips curving round to meet each other; F, stage 16, in which the lateral lips have closed dorsally but are still separated ventrally, where a ventral lip has finally appeared; G and H, showing the variation in shape of the blastopores of neurulae, sometimes a closed dorsoventral slit, sometimes open. Scale line = 0·25 cm.

TABLE 2: Characteristics of Stages 7–11

Stage	External Features	Distribution of Pigment	Segmentation Cavity or Blastocoel	Stage (Semon 1893)	Stages (Kerr 1909)	
					L. paradoxa	*P. annectens*
7 (Fig. 3B, Plate 1G)	cleavage vertical in small pigmented cells, horizontal in large ones	confined to micromeres	space between cells in centre of egg	—	—	—
8 (Fig. 3C, Plate 1H)	irregular and asynchronous cleavage continues; egg rounded	confined to micromeres	space between cells in centre of egg	10	—	—
9 (Fig. 3D, (Plate 1I)	irregular and asynchronous cleavage continues; egg rounded	confined to micromeres	segmentation cavity begins to expand	—	—	—
10 (Fig. 3E)	cleavage continues, large yolky unpigmented cells pressed against vitelline membrane	confined to micromeres	expands further	11	—	IX
11 (Fig. 4A)	egg spherical, small pigmented cells form roof of blastocoel, large unpigmented yolky cells pressed against vitelline membrane	confined to small cells forming roof and sides of blastocoel	attains greatest size	—	9	—

The Fate of the Blastopore

In a young neurula of stage 17, the blastopore is a dorsoventral slit at the posterior extremity of the neural folds (Figs. 4G and H, Pl. 2C). The cleared specimen of stage 21 has a partially divided blastopore (Fig. 6A) but the opening is single in the next stage illustrated (Fig. 6B). The individual of stage 23 (Fig. 6C) has two openings which are quite distinct, one within the neural folds and one just posterior to it. By stage 24, the blastopore, which is single in this specimen, lies inside the neural folds (Fig. 6D). As development proceeds the blastopore grows forward (still within the neural folds), and takes on an oval shape (stages 25–27, Figs. 6E, 7A and B). By stage 27 it has joined the gut cavity. When the neural folds finally close posteriorly a neurenteric canal lined with pigment granules is formed which lengthens as the anus grows forward (stages 27–30, Pl. 2G and H, an Figs. 7B-E). The neurenteric canal persists until stage 34 (Fig. 8D). The behaviour of the blastopore is summarised in Tables 3, 4 and 5.

Formation of the Neural Folds and Early Development of the Brain

This phase of development includes stages 17–30 (see Pl. 2D, E and Figs. 5–7). The neural plate has begun to form by stage 16 before the blastopore is fully developed. The presumptive neural plate flattens at stage 17 (Fig. 5B), and two streaks of darkly pigmented cells extend forwards from the blastopore. By stage 18 the folds are raised anteriorly (Fig. 5C and Pl. 2D). Elevation of the folds and formation of a deep median furrow between the two lines of pigment continues, and at stage 19, the neural folds are easily recognised (Fig. 5D). They are wide anteriorly, with a distinct transverse crest, and low and narrow posteriorly.

This is the stage at which Semon's ectodermal median suture shows occasionally having been found only in the embryos of one season out of nine. Possibly the furrow is a less definite ectodermal median suture without the deep internal folding characteristic of the latter (Semon 1901b; Figs. 7 and 8).

In eggs of stage 20 the transverse crest is deeper and three bilateral swellings, corresponding to the three primary vesicles of the brain, are already present, although the neural folds are still wide open (Fig. 5E). These show best in living eggs, and are well formed by stage 21 (Fig. 6A). The transverse crest sinks inwards and disappears as the two parts of the brain draw together (stage 23,

Pl. 2E and Fig. 6C). The median furrow disappears.

Epithelium covers the anterior neural folds soon after they meet (stage 24, Fib. 6D) and the process continues backwards. The posterior part of the folds is still open at stage 25 (Fig. 6E) and the tip around the blastopore/anus does not close until stage 26 (Fig. 7A and Pl. 2F).

Cleared specimens show that the nervous system of *N. forsteri* forms initially as a tube and never loses its tubular nature. The hollow cavity is lined with granules of egg pigment contained in the part of the nerve cells closest to the cavity. This dark lining persists for a long time (cf. Greil 1908). Formation of the nervous system is summarised in Tables 4, 5 and 6.

Development of the Eye, Auditory Apparatus and Olfactory Organ

The optic vesicles can first be distinguished as a paired hollow outgrowth of the fore brain in cleared specimens of stage 23 (Fig. 6C). By stage 30, the eye is visible externally and a lens is present by stage 32. Pigment appears in the eye at stage 35 just before the rest of the body becomes pigmented.

The auditory apparatus first appears at stage 25 as a deeply pigmented shallow pit on each side of the head (Pl. 2F and Fig. 6E). The pits grow deeper (stages 26 and 27, Figs. 7A and B), sink inwards and become covered by epithelium (stages 28 and 29, Figs. 7C and D). The nervous connection with the brain is present at stage 30 (Fig. 7E) and the ductus endolymphaticus is recognised in cleared specimens by stage 34 (Fig. 8D).

Primordia of the olfactory organ are late to appear. The placodes form as slight depressions on the anteroventral surface of the head at stage 30 (Fig. 7E). They sink inwards and by stage 31 each has a single opening on the external surface rostral to the developing mouth (Fig. 8A). As the upper lip develops, the nares are found at either end of a deep groove at the centre of which is the mouth (stages 37 and 38 — Figs. 10A and B). As the mouth develops the nares are drawn further inwards. The development of the olfactory organs of *N. forsteri* has been described by Bertmar (1965).

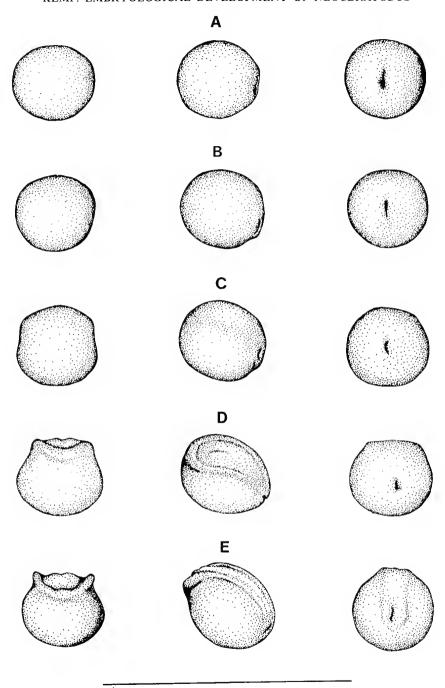Formation of the sense organs is summarised in Tables 5 and 6.

FIG. 5. Early development of the neurula in *N. forsteri*. A series of fixed eggs drawn after removal from the membranes. An anterior view is shown on the left, lateral in the centre and posterior on the right. A, stage 16, showing the almost closed blastopore and the flattened area of the presumptive neural plate; B, stage 17, which is more elongated with a flatter presumptive neural plate and a slit-like blastopore; C, stage 18, showing the lifting of the neural folds anteriorly and the apparently double blastopore; D, stage 19, with neural folds forming anteriorly and a shallow cleft in the centre of the neural plate; E, stage 20, in which the transverse crest and primordia of the primary brain vesicles are visible in anterior view. The blastopore appears to be surrounded by presumptive neural material. Scale line = 1 cm.

TABLE 3: CHARACTERISTICS OF STAGES 12–16

Stage	External Features	Distribution of Pigment	Blastocoel	Blastopore	Stage (Semon 1893)	Stages (Kerr 1909) L. paradoxa	L. annectens
12 (Fig. 4B, Plate 2A)	spherical	present on cells forming roof and walls of blastocoel	very large	long ragged slit at junction of unpigmented yolky cells and small pigmented cells	12	11	XI
13 (Fig. 4C)	spherical	present on cells forming roof and walls of blastocoel	very large	crescentic, position as above; some yolky cells invaginated	13	—	—
14 (Fig. 4D)	spherical	present on cells forming roof and walls of blastocoel	a little smaller	Broad V-shape, most yolky cells invaginated, as well as some cells with pigment, lateral lips slightly drawn in	14	13	XIII
15 (Fig. 4E, Plate 2B)	spherical	all external cells are pigmented, also some invaginated cells; pigment beginning to concentrate in region of future neural plate	a little smaller	lateral lips closing, yolky cells inside, no ventral lip	—	14	XIV
16 (Fig. 4F)	slightly flattened in region of future neural plate	double streak of pigment in region of future neural plate	reduced	lateral lips meet in mid-line dorsally, separate ventrally; ventral lip present	16	—	—
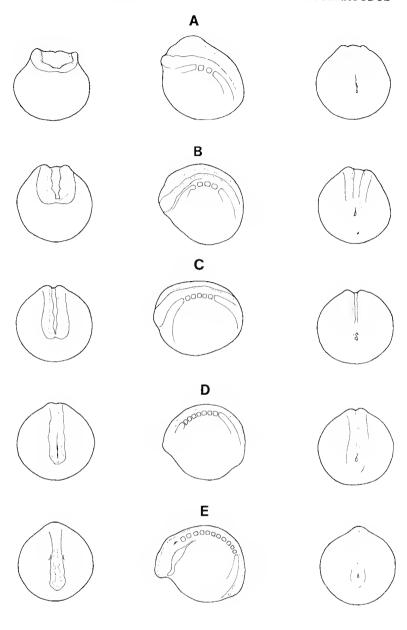
FIG. 6. Drawings of cleared eggs showing later development of the neurula. The anterior view is shown on the left, lateral in the centre and posterior on the right. A, stage 21, with the neural folds closer anteriorly than posteriorly, blastopore partly outside the neural folds, transverse crest and fore, mid and hindbrain vesicles, and two somites; B, stage 22, showing the distinct primary brain vesicles, transverse crest sinking inwards, 3 somites and the slit-like blastopore; C, stage 23, an embryo of 5 somites in which the neural folds are nearly closed anteriorly, the apparently double blastopore partly enclosed in the folds posteriorly and early indications of the opticoele; D, stage 24, with neural folds closed anteriorly and open posteriorly where they surround the now single blastopore; seven somites are present and the telencephalon, diencephalon, with associated opticoeles, mesencephalon, metencephalon, and myelencephalon can be distinguished; E, stage 25, in which ectoderm has covered all but the most posterior part of the neural folds, the opticoele is more distinct, neuromeres are present in the hindbrain, the otic placode has appeared, there are 11 somites and the oval blastopore is surrounded by neural material. The archenteron has expanded anteriorly to form the pharynx. Scale line = 1 cm.

Development of the Lateral Line System

The lateral line system of the trunk begins to form at stage 41 (Pl. 3B and Fig. 12A), and extends along the body (Figs. 12B and C and Table 8). At stage 44 it reaches the tail tip (Fig. 13A). There is a slight flexure in the tail region.

The development of the lateral lines and pits of the head of *N. forsteri* has been followed in reconstructions of developing embryos and larvae by Pehrson (1949). The present work is concerned only with those parts that are easily visible externally and therefore useful for estimation of the stage of development of larvae (Tables 8 and 9).

At stage 44 (fish from Enoggera Reservoir) and stage 43 (river fish) sensory lines appear above and below the eye (Fig. 13A). By stage 45 (Fig. 13B), the main lines of the head are established, as follows: in side view the supra- and infraorbital, in ventral view the mandibular and dorsally the temporal and posterior head lines (Pehrson 1949). The jugal line forms at stage 46 (Fig. 13C). By the next stage the supratemporal cross commissure has formed and the distinct lines have broken up into separate pits (Pl. 3D and Fig. 14A). The oral line is not visible until stage 49 (Fig. 15A). The lateral line system of the head is soon obscured by increasing pigmentation in the skin.

Appearance of the Myotomes

In embryos of stage 20 the mesoderm is undivided. By stage 21, before the neural folds close, two somites are present (Fig. 6A) and somites are added in front and behind the first two, up to stage 24 (Fig. 6D), after which they are added only posteriorly. The V-shape of the myotomes develops by stage 33 (Fig. 8C). Numbers of somites at the various stages are included in Tables 4, 5, 6 and 7.

The Pronephros

The pronephros is distinguishable externally as a prominent bulge just behind the auditory placode from stage 27 (Fig. 7A and Table 5) onwards and in cleared specimens it is associated with postotic somites 4, 5 and 6 (stage 30, Fig. 7E and Table 6 and stages 31–34, Figs. 8A–D). At stage 32 it appears as two tubules and a short duct (Fig. 8B and Table 6), which has grown towards the tail by stage 33 (Fig. 8C). The whole organ has moved posteriorly in relation to the somites at stage 35 (Fig. 9A and Table 7). Subsequently it becomes difficult to distinguish externally and loses its usefulness as a guide to stage of development. Further details of pronephric development may be found in the series of papers by Fox (1960, 1961 and 1962).

Development of the Mouth

Up to stage 28, there is little sign of mouth development. The presumptive mouth region is smooth and uncontoured until stage 29, when an indentation develops on the anteroventral surface of the head (Fig. 7D). At stage 33 (Fig. 8C) a triangle of pale endoderm shows through the ectoderm of the mouth region. At stage 34 the mouth cavity grows deeper and at stage 35 the upper lip begins to form, gradually involving the nares at the lateral borders (Figs. 8D, 9A, 9B and 10A). The lower lip starts to develop at stage 38 as the mouth cavity grows deeper (Fig. 10B). At stage 41 the foregut and mouth cavities join. The lower lip grows forwards, meeting the upper at stage 45 (Figs. 12 and 13). The mouth shifts anteriorly, becoming terminal at stages 51–52 (Figs. 16A and B). By stage 54, differential growth has left the mouth in a slightly subterminal position, as in the adult, with the lower jaw fitting within the upper and the anterior openings of the nares showing inside the upper lip (Fig. 17B). Gular pits develop behind the lower lip at stages 46–47 (Fig. 13C and 14A).

These phases of development are summarised in Tables 6, 7, 8, 9 and 10.

Formation of the Archenteron and the Gut

Towards the end of the period of neural tube formation (stage 25, Fig. 6E) the archenteron is wide anteriorly and very narrow behind. By stage 27 the posterior section is slightly distended. The anus is linked with the posterior end of the nerve cord as well as the gut (Fig. 7B). Anteriorly the foregut is growing forward but the mouth has not yet appeared. The liver diverticulum develops at stage 33 (Fig. 8C) and the neurenteric canal disappears at stage 34 (Fig. 8D).

Until stage 31, the endodermal cell mass remains globular and the head extends forwards, but after stage 32, the endodermal cell mass progressively loses its round shape as the body axis lengthens and the tail bud grows. At stages 37–38 (Pl. 3A) the endodermal cells, still laden with yolk, are packed together in platelet fashion and these show through the epidermis.
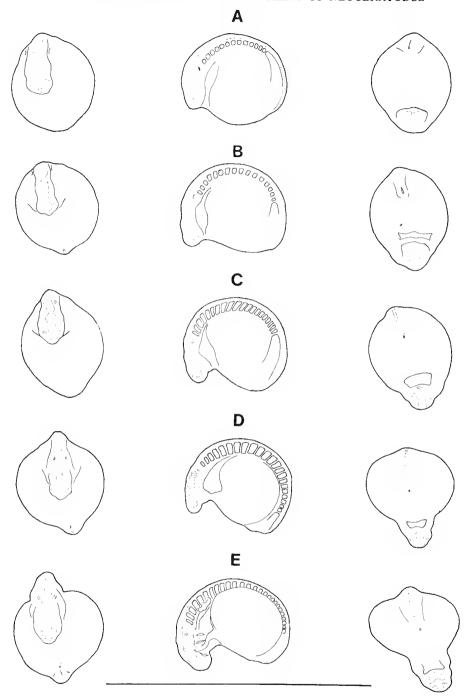
FIG. 7. Cleared embryos of *N. forsteri* showing development of the head region. Anterodorsal view on the left, lateral in the centre and ventral on the right. A, stage 26, with opticoeles, otic placode, pronephros, 13 somites, neurenteric canal and pharynx. B, stage 27, with 16 somites and the blastopore (anus) continuous with the gut and the neural tube; C, stage 28 showing further development of the opticoeles, formation of the otic capsule and 20 somites; D, stage 29 with dorsal root ganglia and 22 somites; the anus has grown forward along the mid-ventral line and the neurenteric canal has grown with it; E, stage 30, with 26 somites, 2 gill slits, olfactory placode close to the developing mouth and pronephros associated with post-otic somites 4, 5 and 6. Scale line = 1 cm.

TABLE 4: CHARACTERISTICS OF STAGES 17–22

Stage	Blastopore	Nervous System	Somites	Stage (Semon 1893)	Stage (Kerr 1909) L. paradoxa	P. annectens
17 (Fib. 5B, Plate 2C)	single dorso-ventral slit; partly within neural folds	indicated by concentration of pigment cells and flattening of egg dorsally	—	—	—	—
18 (Fig. 5C, Plate 2D)	single dorso-ventral slit; partly within neural folds	greater concentration of pigment cells, more flattening, raising of neural folds anteriorly	—	17	—	XVI
19 (Fig. 5D)	single dorso-ventral slit; partly within neural folds	raising of neural folds progresses posteriorly, medium furrow in centre of plate in some eggs	—	18	—	—
20 (Fig. 5E)	single dorso-ventral slit; partly within neural folds	transverse crest and indications of the 3 primary brain vesicles are present; folds are wide open	block of undivided mesoderm	19	16	—
21 (Fig. 6A)	apparently double; upper opening in neural folds, lower outside	transverse crest, fore-, mid- and hind-brain readily visible	2	20	—	—
22 (Fig. 6B, Plate 2E)	single, not completely surrounded by folds	folds raised almost to blastopore and closer together, no medial cleft; transverse crest sinking, hind brain begins to divide into two parts	3–4 somites are formed at anterior and posterior ends of mesoderm block	22	—	—
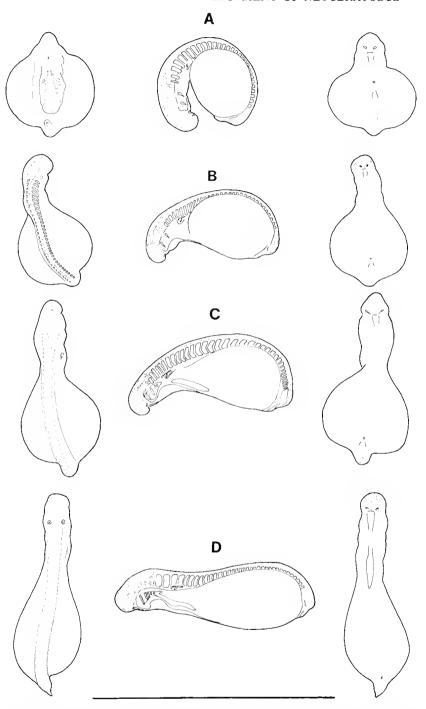
FIG. 8. Drawings of cleared specimens of late neurulae. Anterodorsal view on the left, lateral in the centre and ventral on the right. A, stage 31, in which all the structures present in stage 30 are larger and more defined, the endoderm is globular and there are 30 somites; B, stage 32, the embryo is growing longer with 33 somites and a pronephros with two tubules and a duct; C, stage 33, showing the developing mouth, the liver diverticulum of the foregut, four gill slits and 35 V-shaped somites; D, stage 34, with a distinct pronephros, 36 somites, neurenteric canal in the process of disappearing, a fifth gill slit, endolymphatic duct, deepening mouth cavity and developing nares. Scale line = 1 cm.

Yolk in endodermal cells is reduced considerably by stage 43 (Pl. 3C), although some yolk is still present at stage 47, when the form of the spiral valve becomes clear (Fig. 14A). Yolk has disappeared from the gut by stage 49, when the spiral valve is well formed (Fig. 15A). The rectum, which forms at right angles to the rest of the gut, shows clearly from stage 38 onwards (Fig. 10B). Development of the gut and associated structures is summarised in Tables 6, 7, 8 and 9.

THE GILL CLEFTS AND THE OPERCULUM

The gill clefts show externally at stage 30 (Fig. 7E) as they are situated on a prominent bulge on either side of the head and connect with the pharynx. There are 4 clefts by stage 33 and 5 at stage 34 (Figs. 8C and D). The operculum is present at stage 36 as a fold of epithelium between the first two gill clefts (Fig. 9B). The second cleft is covered at stage 37 (Fig. 10A) and the third at stage 38 (Fig. 10B). By stage 41 all four posterior slits are beneath the operculum (Fig. 12A). The operculum develops behind the first cleft and never covers it. Externally, the gill clefts do not yet appear to be open. At stage 44 the opercular folds meet midventrally (Fig. 13A).

FORMATION OF THE PAIRED FINS

Incipient pectoral fins are first recognised at stage 42 in lake fish (Pl. 3B and Fig. 12B) as tiny unpigmented primordia, one on each side of the body immediately behind the free edge of the operculum (Table 8). Pigment cells appear in the growing fin at stage 43 (Pl. 3C). By stage 45 the fins are larger and the anterior part is covered by backward growth of the opercular folds (Fig. 13B and Table 9). The skeleton of the fin can be seen in specimens of stage 47 (Fig. 14A). The pectoral fins do not appear until stage 44 in river fish.

The pelvic fins develop in a similar manner but appear slightly later, at stage 48 (Fig. 14B and Table 9) in lake fish. Pigment cells appear in the fin at stage 49 and the skeleton shows at stage 51 (Fig. 15C and Table 10). Pelvic fins do not appear until stage 50 in river fish.

DEVELOPMENT OF THE MEDIAL FINS

At stage 35 the tail bud (Pl. 2J and Fig. 9A) straightens and begins to grow larger. A dorsal median fin, one third of the length of the trunk, is present at stage 36 (Fig. 9B). By stage 37 there is a small median ventral fin and the dorsal fin, now half the length of the trunk (Pl. 3A and Fig. 10A), reaches its greatest length relative to the trunk at stage 38 (Fig. 10B), extending as far as the back

of the head; a pre-anal ventral fin also appears. All three fins grow in subsequent stages (Fig. 11–14). At stage 49, skeletal elements can be distinguished in both the dorsal and post-anal ventral fins, but they never develop in the pre-anal ventral fin, which grows forward as far as the operculum (Fig. 15A) by stage 49 and thereafter regresses. It disappears by stage 53 (Fig. 16B). The dorsal fin also undergoes some regression, extending forward only as far as the middle of the trunk at stage 54 (Pl. 3H and Fig. 17B). Development of the medial fins is summarised in Tables 7, 8, 9 and 10.

FORMATION OF THE SCALES

Scales appear late, at stage 52 (Table 10) beginning as primordia regularly distributed over the body surface under the epidermis. They are well established by stage 54. The scales illustrated by Semon in his larva of stage 45 have not been observed at an equivalent stage in the present material.

DEVELOPMENT OF PIGMENT

Adults of *Neoceratodus forsteri* are characterised by two main pigments, melanin and a red pigment. Melanin (within melanophores) is the first to appear (stages 36–37, Pl. 3A), becoming widespread over the body by stage 42. The melanophores have the property of expansion and contraction in response to external light and dark illumination while the animal is young (cf. *L. paradoxa*, Kerr 1900).

River juveniles are pale brown and mottled, (Pl. 3H), and lake juveniles are usually dark brown. Spots of intense dark pigment on the dorsal fin are common. Cells containing a different pigment, red in living animals and colourless in fixed specimens, appear at stage 43 (Pl. 3C). They are larger than the melanophores. At first they are confined to the dorsal surface but as more develop they spread ventrally until they are scattered all over the body. Pigment formation is summarised in Tables 7, 8, 9 and 10.

THE INTRAVITELLINE SPACE AND THE PROCESS OF HATCHING

There is little change in the dimensions of the embryo, apart from those alterations in shape associated with cleavage and development of the blastula, gastrula and the neurula, until the head begins to extend forwards, at about stage 28. The head continues to grow, but the vitelline membrane does not start to expand until stage 32. Though capable of movement when removed from the membranes, the embryo lies inert in the
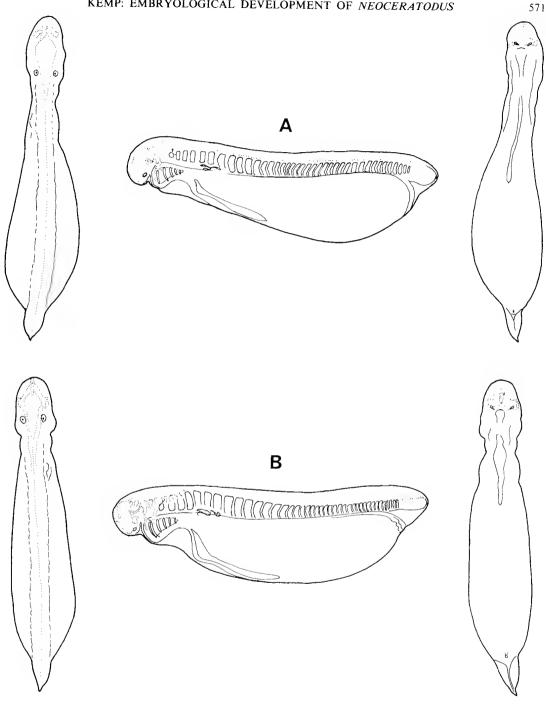
FIG. 9. Later neurulae drawn from cleared specimens. Dorsal view on the left, lateral in the centre and ventral on the right. A, stage 35, with 37 somites, less distinct pronephros showing two tubules and a duct, initial development of the upper lip, the rectum and the tail bud and continued elongation of the endodermal mass; B, stage 36, showing 40 somites and further development of the tail bud, rectum and mouth cavity and the appearance of the opercular fold. Scale line = 1 cm.

capsule with the head bent round to the anus. At stage 32, the space within the membranes starts to expand, and the embryo becomes more active. Large cracks appear in the vitelline membrane at stage 35–37 (Pl. 1B). The embryo moves more freely and soon the vitelline and inner albumen membranes break down completely and the outer albumen membrane is dissolved from within, thus enlarging the cavity in which the fish lives. The broken membranes lie in pieces at the bottom of the egg capsule.

Hatching occurs between stages 43–46 when a small hole appears in the albumen capsule and the young fish can escape.

ASSUMPTION OF THE ADULT FORM AND HABITS

The globular shape of the endodermal mass disappears at stage 31–34 as the body extends and the number of somites increases. A proper tail starts to grow at stage 36–37 (Pl. 3A). The adult form develops gradually as the fins appear and assume the adult sizes and proportions (Pl. 3E–H). There is no obvious metamorphosis.

For a long time the body of the juvenile is very thin (between stages 44 and 54), giving the animal a peculiar appearance in dorsal or ventral view. Young fish (Pl. 3G and Figs. 16 and 17) are much slimmer than adults but gradually the trunk becomes thicker and the body form of the adult appears.

Larvae of stage 52 have been observed to breathe air in laboratory aquaria.

DISCUSSION

Eggs of *Neoceratodus forsteri* have a thick albumen coat apparently like *Protopterus dolloi* (Pasteels 1962: 175) but unlike *Lepidosiren paradoxa,* which usually has no jelly (Kerr 1900: 308). Kerr suggests that this is because *L. paradoxa* eggs develop in the comparative security of a guarded nest. However *P. dolloi* eggs also develop in a nest and the function of the jelly remains unknown. The hatching process, involving breakdown of the inner membranes, also requires further elucidation.

The eggs of all three lungfish are very large compared with those of many Amphibia, and possess large amounts of yolk (Kerr 1919). The eggs of *L. paradoxa* are spherical, 6·5–7 mm in diameter with pink yolk and a white germinal cap of more finely divided yolk. There is no dark pigment in the eggs (Kerr 1900: 308). *P. annectens* lays smaller eggs, also spherical, with a diameter of 3·5–4 mm which have green yolk and

a pink epiblastic pole (Budgett 1901). Pasteels (1962: 175) describes the eggs of *P. dolloi* as 4 mm in diameter, yellowish cream in colour and entirely without pigment. The animal pole of living eggs has a rosy tint and the vitelline mass is greenish. Eggs of *N. forsteri* are the smallest, 3–3·5 mm in diameter, hemispherical in shape with green or brown yolk granules. They have granules of dark pigment, usually in the uppermost parts of the egg. Possibly this protects the eggs as they often develop in situations exposed to light, an adaptation which is not necessary for the eggs of other lungfish which develop in dark underwater burrows.

In eggs of *N. forsteri,* pigment is scattered sparsely over most of the egg surface and is dense only in a small area. Cleavage is usually initiated in this area, no matter where it is on the egg i.e. round or flat surface. Many abnormalities in cleavage can be traced to the unusual position of pigment on the egg. The animal pole appears not to be that part of the egg which is flat and floats uppermost, but is the region that has the bulk of egg pigment; the vegetal pole is the part of the egg most free of these granules. Usually, the pigment and therefore the animal pole is on the flat surface which is uppermost.

Various external features that are prominent in some newly fertilised eggs may be compared with those in some amphibians. For example the dark spot may correspond to the point of sperm entry and the pale area mark the position of the oocyte or zygote nucleus. There is, however, little evidence to support these ideas. The dark spot is found in some uncleaved eggs and soon disappears. The pale area is shared out among cleavage products in eggs which possess one, but their nuclei are not superficial in position either at the beginning of cleavage or later, while the pale area persists. Nuclei lie well below the surface between the small peripheral yolk granules and the large central yolk granules.

It is still possible that the pale area corresponds to the position of a superficial oocyte nucleus, but if so it is difficult to explain the persistence of the pale area after the nucleus moves inwards. Alternatively the pale area may mark the position of sperm entry and function like the grey crescent of certain amphibian eggs. If this is true the pale area should be found in a position on the surface of the blastula equivalent to its position in the uncleaved egg. However it is split up and shared out to cleavage products and cannot be traced after stages 3 or 4.
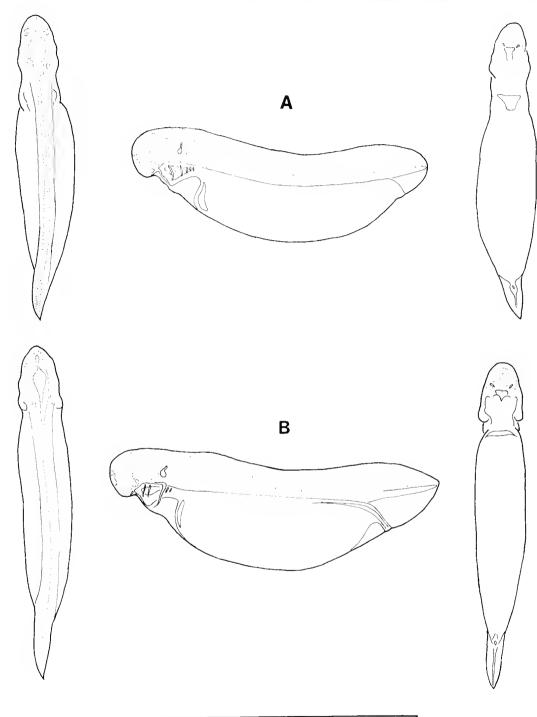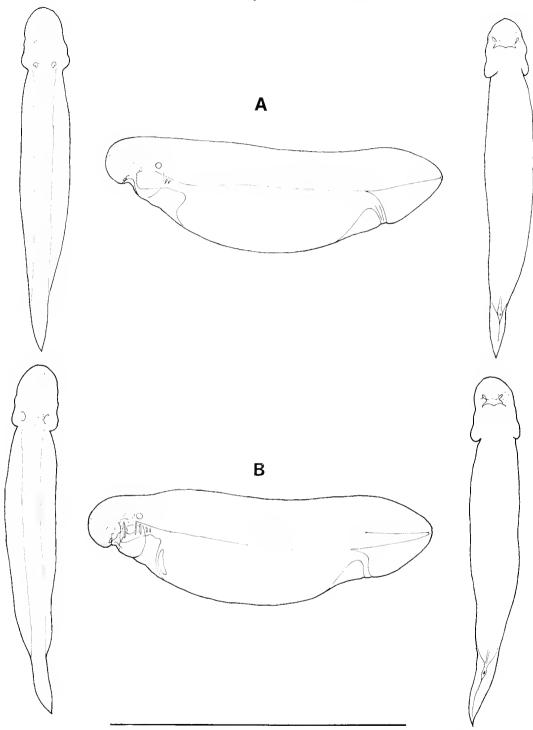
FIG. 10. Drawings of cleared specimens showing the development of the median fins. Dorsal view on the left, lateral in the centre and ventral on the right. A, stage 37, showing the development of the dorsal fin and the ventral post-anal fin as the body extends, and the growth of the opercular fold and upper lip (involving the nares); B, stage 38, with the initial development of the ventral pre-anal fin, dorsal fin reaching the back of the head, growth of the opercular fold to cover the anterior gill slits and the appearance of the lower lip. Scale line = 1 cm.

FIG. 11. Drawings of cleared specimens showing growth of the median fins. Dorsal view on the left, lateral in the centre, and ventral on the right. A, stage 39, operculum covering anterior 3 gill slits, forward growth of the lower lip, continuing involvement of the nares in the formation of the upper lip, development of the rectum and increasing length of the tail; B, stage 40, showing primordium of the trunk lateral line behind the operculum. Increasing density of the melanophores in the skin makes it less rewarding to examine cleared specimens. Scale line = 1 cm.

Abnormalities of cleavage in *N. forsteri* are common and do not always prevent subsequent development. Obviously some types of abnormal cleavage are more detrimental to development than others but the number of eggs of unusual pattern available was not great enough to compare individual abnormalities with normal eggs.

Many of the unusual patterns of cleavage may be directly related to the region of the egg in which the pigment is located, but some are more difficult to explain, for example a three cornered division or latitudinal first cleavage. It would be interesting to know if abnormal patterns in early cleavage are found in other lungfishes or in Amphibia, with similar frequencies and as little effect on later development. Miller (1923) found some irregular patterns in *L. paradoxa*. Unusual cleavage patterns, whatever their cause, disappear when the blastocoel expands and the egg prepares for gastrulation.

The blastocoel increases in size until the egg fills the whole intravitelline space and is no longer able to rotate. It is possible that the egg needs the mechanical support of the vitelline membrane for normal gastrulation movements to occur. Previous descriptions of gastrulation in *N. forsteri* (Semon 1893, 1901a) have not shown details of the change from a crescentric dorsal lip lying across the egg (midgastrula) to a dorsoventrally orientated slit (early neurula).

Examination of a complete series of fixed and living embryos in the process of gastrulation suggests that the mode of formation of the blastopore is similar in *N. forsteri, P. dolloi* and Amphibia, particularly Urodela (Anderson 1943; Weisz 1945; Eakin 1947; Rugh 1962). In the Queensland lungfish, the curved dorsal lip appears early and there is little external change for a long time (Stages 12–13). Wide lateral lips form next. The ventral lip normally develops very late after the drawing together of the lateral lips has almost converted the blastopore into a dorsoventral slit (Stages 14–16). These stages are transient. A common variation, which does not hamper future development, results in a large yolk plug like that of an amphibian embryo (for example, a Stage 12 embryo of *Triturus pyrrhogaster,* Anderson 1943). In addition, there is a close external similarity between *N. forsteri* and *T. pyrrhogaster* gastrulation in later stages.

In *P. dolloi,* the blastopore is at first a slit, then crescentic, as in *N. forsteri.* Later, after the invagination of the yolky cells, it is ring-shaped with the dorsal and ventral lips in apposition, lying transversely across the egg (Pasteels 1962: 177).

The condition in *L. paradoxa* (Kerr 1900, plate 8, figs. 12, 13 and 14 and plate 9, fig. 15) and in *P. annectens* (Budgett 1901 plate 10) appears to be similar. Differences in gastrulation in *N. forsteri, P. dolloi, P. annectens, L. paradoxa* and amphibians appear to be minor, involving the shape of the blastopore, and the time taken for the yolky cells to be invaginated and for the ventral lip to appear.

Changes in the shape of the blastopore of fixed specimens of successive stages probably reflect no more than the plasticity of the blastoporal lips in the living egg, i.e. moving in and out and sometimes joining to produce two openings, one within and one outside the neural folds. The blastopore ultimately gives rise to the anus, as in *L. paradoxa* (Kerr 1900: 313), and it is linked for a long time to the nerve cord via the neurenteric canal, a feature absent in *L. paradoxa* (Kerr 1900: 312).

It is curious that the globular portion of the endodermal cell mass is positioned under the head region in *L. paradoxa* and *P. annectens* and more posteriorly in *N. forsteri* (Kerr 1909).

The neural rudiment in *L. paradoxa,* as in lampreys and teleostomatous fishes, forms by the downgrowth of the medullary plate as a solid keel of tissue (Kerr 1902: 22; 1919: 83) and the central cavity characteristic of vertebrate nervous systems develops later either by the appearance of a fine intercellular split or by the breakdown of cells along the axis. However, traces of the formation of the spinal cord by the meeting of two folds may be found (Kerr, 1902: 23 and Pl. 4). The nervous system of *N. forsteri* is always tubular (Greil 1908).

The primary vesicles of the brain in *N. forsteri* appear before the neural folds have closed, and in *L. paradoxa* and *P. annectens* they do not develop until after the folds close (Kerr 1909), but this is not a fundamental difference. The presence of a distinct transverse crest linking the anterior neural folds in embryos of stage 20–23 in *N. forsteri* is reminiscent of urodele development (Anderson 1943).

Many aspects of early development in *N. forsteri* are similar to those of amphibian embryos e.g. the arrangement of cleavage furrows, formation of the blastopore, appearance of a transverse crest in the anterior neural plate, development of the nerve cord as a tube and the shape of the embryos. However such similarities are common among diverse lower vertebrate groups. Parallels may equally well be drawn between the arrangement of cleavage furrows in

TABLE 5: CHARACTERISTICS OF STAGES 23–28

Stages	Blastopore /anus	Nervous System	Sense Organs	Somites	Pronephros	Stage (Semon 1893)	Stage (Kerr 1909) L. paradoxa	P. annectens
23 (Fig. 6C)	2 openings, upper within neural folds, lower outside	folds raised almost as far as the blastopore and closer together, no furrow in centre, transverse crest sinks further	first indication of opticoele in cleared specimens	5; form at anterior and at posterior end of mesoderm block	—	24	18	XVIII
24 (Fig. 6D)	single, upper part within neural folds	transverse crest gone, folds closed anteriorly, raised around blastopore	opticoele distinct in cleared specimens	7	—	26	20	—
25 (Fig. 6E)	single, not continuous with neural canal	neural rudiment hollow folds still open at posterior extremity	opticoele develops, auditory placode shows externally as pigmented pit	10–11, new somites form only at posterior end from this stage	—	27	—	XX
26 (Fig. 7A, Plate 2F)	continuous with neural canal	folds entirely covered in epithelium	auditory placode sinks inwards	13	—	28	21	—
27 (Fig. 7B)	blastopore (anus) continuous with gut cavity and neural canal	fore-brain separates into two parts	opticoele more distinct from brain	15–17	visible externally as small bulge behind auditory vesicle	29	—	XXI
28 (Fig. 7C)	blastopore (anus) continuous with gut cavity and neural canal		auditory vesicle close to metencephalon	18–20	—	—	23	—

Acipenser and in *N. forsteri* (Kerr 1919: 24) or between gastrulation and the general shape of embryo in lungfish and lampreys (Balfour 1881: 73 and Kerr 1919: 38).

The appearance of a pre-anal ventral fin at stage 38 and its growth and subsequent regression by stage 53 is a curious feature for which no parallel can be found in fossil or living Dipnoi, though some fossil specimens seem to have had separate post-anal ventral fins *(Dipterus valencienesi,* Forster-Cooper 1937, *Fleurantia denticulata,* Graham-Smith and Westoll 1937 and *Phaneropleuron andersoni,* Dollo 1895). Certain young Amphibia possess traces of a pre-anal fin for example Urodela like *Ambystoma punctatum* (stage 40) and *Taricha torosa* (stage 39) (Rugh 1962) and Anura like *Hyla regilla* (stages 23 and 24) (Eakin 1974) and *Xenopus laevis* (stages 20–23) (Weisz 1945). The transient appearance of a double flap of skin in front of the anus in the mid-ventral line is not a firm basis for suggesting links between lungfish and amphibia but it is a further point of similarity in the external features of their young forms.

Close similarity in external appearance between *N. forsteri* and amphibian embryos ends at stage 42 when the pectoral fins appear and specifically dipnoan characteristics become increasingly recognisable.

The times of appearance of the pectoral fins at stage 42 and the pelvic fins at stage 48 in the present material do not agree with those given by Semon (1893) who found pectoral fins at his stage 45 and pelvic at his stage 47. This may reflect a genetic difference in the embryos or perhaps variation in the conditions under which the animals were reared. Also at a stage in the present series corresponding to Semon's stage 45, in which he described scales, no scales were found. The primordia of scales in this material were not apparent externally until stage 53 and were not easy to see until stage 54.

Differences in the external features of developing *N. forsteri* from the Brisbane River and Enoggera Reservoir are minor — the shape of the cleaving egg and the times of appearance of the pectoral and pelvic fins and the sensory lines of the head.

Juveniles of all three genera of lungfish begin to breathe air at approximately the same stage of development; *P. annectens* when it is 25 mm long (Johnels and Svensson 1955), *L. paradoxa* at 30 mm (Kerr 1900) and *N. forsteri* at 25 mm (stage 52). Young fish also respond to light in a similar way (Kerr 1900), though *N. forsteri* juveniles lose

this ability when the skin pigment becomes uniformly dark over the dorsal surface.

Unlike most members of the Amphibia, there is no obvious metamorphosis in *N. forsteri*. The animal gradually assumes an adult form without sudden changes.

The number of stages in the present work is seven more than in Semon's account (1893) but five of these are older than his latest stage. There are also more stages than given by Kerr (1909). Older specimens are included in the present work as well as more cleavage and gastrulation stages. It is often important in a living embryo to be able to estimate as precisely as possible the stage of development from external appearances. These features have been emphasised in this account.

ACKNOWLEDGEMENTS

LITERATURE CITED

ANDERSON, P.L. 1943. The normal development of *Triturus pyrrhogaster*. *Anat. Rec.* **86**: 59–63.

BALFOUR, F.M. 1881. 'Treatise on Comparative Embryology.' vol. II. (London: MacMillan and Co. Ltd.).

BERTMAR, G. 1965. The olfactory organ and upper lips in Dipnoi, an embryological study. *Acta Zool.* **46**: 1–40.

BUDGETT, J.S. 1901. On the breeding habits of some West African fishes with an account of the external features in the development of *Protopterus annectens* and a description of the larva of *Polypterus lapradei*. *Trans. Zool. Soc. London* **16**: 115–36.

DOLLO, L. 1895. Sur la phylogenie des Dipneustes. *Bull. Soc. belge., Geol. Palaeont. Hydrol.* **9**: 79–128.

EAKIN, R.M. 1947. Determination and Regulation of polarity in the retina of *Hyla regilla*. *Univ. Calif. Publs. Zool.* **51**: 245–88.

FORSTER-COOPER, C. 1937. The middle Devonian fish fauna of Achanarras. *Trans. Roy. Soc. Edinb.* **59**: 223–39.

FOX, H. 1960. Early pronephric growth in *Neoceratodus* larvae. *Proc. Zool. Soc. London* **134**: 659–63.
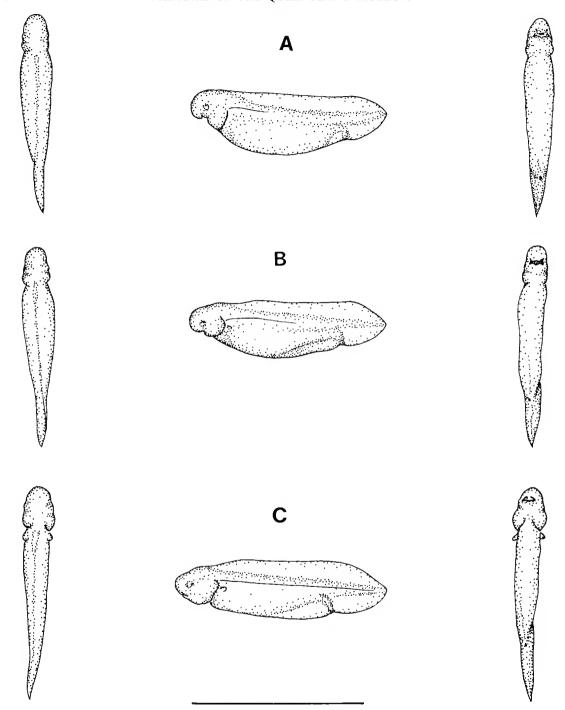
FIG. 12. Drawings of the embryos removed from the egg membranes before fixation showing the growth of the trunk lateral line and the appearance of the pectoral fin. Dorsal view on the left, lateral in the centre and ventral on the right. A, stage 41, showing operculum covering all the gill slits, forward growth of the lower lip and lateral line extending one-third of the way down the body; B, stage 42, in which the lateral line extends halfway down the body and the primordium of the pectoral fin appears; C, stage 43, with a longer lateral line stopping short of the tip of the tail, larger pectoral fin, and nares still visible in the upper lip. Scale line = 1 cm.

1961. The segmentation of components in the hind region of the head of *Neoceratodus* and their relation to the pronephric tubules. *Acta. Anat.* **47**: 156–63.

1962. A study of the evolution of the amphibian and dipnoan pronephros by an analysis of its relationship with the anterior spinal nerves. *Proc. Zool. Soc. London* **138**: 225–56.

GRAHAM–SMITH, W. and T.S. WESTOLL, 1937. On a new long headed dipnoan fish from the Upper Devonian of Scaumenac Bay, P.Q., Canada. *Trans. Roy. Soc. Edinb.* **59**: 241–66.

GREIL, A. 1908. Entwickelungsgeschichte des Kopfes und des Blutgefass systems von *Ceratodus forsteri*. Erster Theil: Gesammentwickelung bis zum beginn der Blutcirculation. *Denkschr. med.–naturw. Ges. Jena.* **4**: 661–934.

GÜNTHER, A. 1871. Description of *Ceratodus,* a genus of ganoid fishes recently discovered in rivers of Queensland, Australia. *Phil. Trans. Roy. Soc.,* B **161**: 511–71.

JOHNELS, A.G. and G.S.O. SVENSSON, 1955. On the biology of *Protopterus annectens* (Owen). *Ark. Zool.* 7:134–64.

KEMP, A. 1981. The growth rate of larvae of the Australian lungfish, *Neoceratodus forsteri* (Krefft) under laboratory conditions. *Copeia* **1981** (4): 776–84.

KERR, J.G. 1900. The external features in the development of *Lepidosiren paradoxa* Fitz. *Phil. Trans. Roy. Soc.,* B **192**: 299–330.

1902. The development of *Lepidosiren paradoxa.* Part II. With a note on the corresponding stages in the development of *Protopterus annectens. A. J. Microsc. Soc.* **45**: 1–40.

1909. Normal plates of the development of *Lepidosiren paradoxa* and *Protopterus annectens. Normaltafeln z. entw. gesch. Wirbelt.* **10**: 163–94.

1919. 'Textbook of Embryology.' vol. 11. Vertebrata. (London: MacMillan and Co. Ltd.).

KREFFT, G. 1870. Description of a giant amphibian allied to the genus *Lepidosiren* from the Wide Bay district, Queensland. *Proc. Zool. Soc. London* **1870**: 221–4.

MILLER , A.E. 1923. the cleavage of the egg of *Lepidosiren paradoxa. Q. J. Miscrosc. Sci.* **67**: 497–505.

PASTEELS, J. 1962. Gastrulation du *Protopterus dolloi* Boulenger. *Annls. Mus. r. Afr. cent.* scr. 8vo **108**:173–83.

PEHRSON, T. 1949. The ontogeny of the lateral line system in the head of dipnoans. *Acta Zool.* **30**: 153–82.

RUGH, R. 1962. 'Experimental Embryology. Techniques and Procedures.' (Minnesota: Burgess Publishing Co.).

SEMON, R. 1893. Die aussere Entwickelung des *Ceratodus forsteri. Denkschr. med.–naturw. Ges. Jena* **4**: 29–50.

1901a. Die furchung und Entwickelung der Keimblatter bei *Ceratodus forsteri. Denschr. med–naturw. Ges. Jena* **4**: 301–32.

1910b. Die 'ectodermal Mediannaht' des *Ceratodus. Arch. Entw. Mech. Org.* **11**: 310–20.

WEISZ, P. 1945. The development and morphology of the larva of the South African clawed toad, *Xenopus laevis. J. Morph.* **77**: 163–217.

TABLE 6: CHARACTERISTICS OF STAGE 29–33

Stage	External Features	Nervous System	Sense Organs	Somites	Pronephros	Stage (Semon 1893)	Stage (Kerr 1909) L. paradoxa	Stage (Kerr 1909) P. annectens
29 (Fig. 7D)	expanded anterior cavity, very narrow canal reaches anus; first external sign of mouth	neurenteric canal present, dorsal root ganglia develop	auditory vesicle close to hind brain	24, oblong shape	visible externally behind auditory vesicle	—	—	XXIII
30 (Fig. 7E, Plate 2G)	2 visceral clefts endodermal mass globular	thin roof of hind brain shows	eye visible externally, auditory vesicle linked with auditory nerve, first sign of olfactory placodes anterior to mouth region	26	in cleared specimens associated with post-otic somites 4, 5, and 6	30	25	—
31 (Fig. 8A)	mouth is a little deeper	expansion and forward growth of brain	olfactory placodes sink	30	in cleared specimens associated with post-otic somites 4, 5, and 6	32	—	XXV
32 (Fig. 8B, Plate 2H)	as long axis of body begins to grow, endodermal mass less globular	expansion and forward growth of brain	olfactory capsule open to exterior	33	compact organ, 2 nephrotomes and duct	34	—	—
33 (Fig. 8C, Plate 21)	liver diverticulum forms, 2 more visceral clefts appear mouth is a tri-angular area of pale endoderm showing through epithelium	expansion and forward growth of brain	—	35 V-shaped	duct grows posteriorly	36	27	XXVII
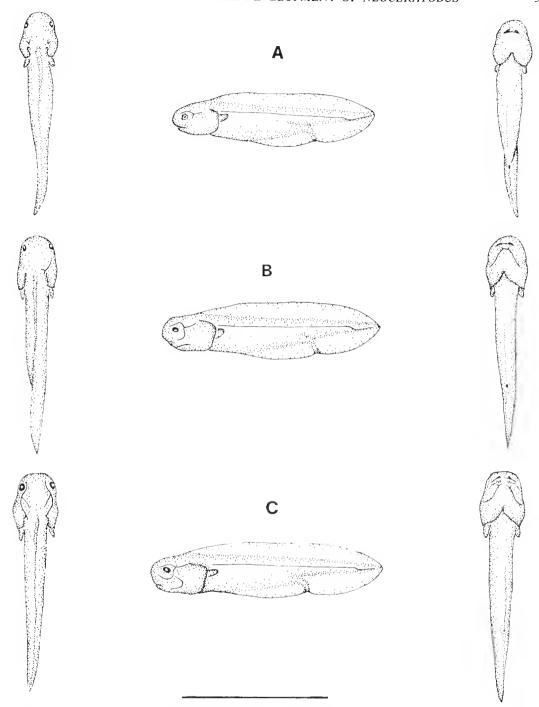
FIG. 13. Development of the pectoral fin and appearance of the sensory lines of the head. Dorsal view on the left, lateral in the centre, and ventral on the right. A, stage 44, in which the pre-anal ventral fin is growing forwards and the dorsal reaches the back of the head. The lateral line of the trunk reaches the tail tip. Infra- and supra-orbital head lines are present; B, stage 45, showing two more sensory head lines dorsally, the temporal and posterior lines, and one ventrally, the mandibular; yolk is still present in the gut and much of the pectoral fin is overgrown by the operculum; C, stage 46, with links forming between the sensory head lines, jugal line and gular pits beginning to form behind the lower lip. The mouth has shifted anteriorly. Scale line = 1 cm.

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TABLE 7: CHARACTERISTICS OF STAGES 34–38

| Stage	Gut	Medial Fins	Chromatophores	Somites	Pronephros	Stage (Semon 1893)	Stage (Kerr 1909) L. paradoxa	P. annectens
34 (Fig. 8D)	neurenteric canal still present, mouth grows a little deeper, 5 gill clefts present	tail bud		36	Pronephros prominent externally	37	—	—
35 (Fig. A, Plate 2J)	neurenteric canal disappears, upper lip begins to develop, as tail bud straightens and embryo grows longer the globular shape of the yolk is lost	tail bud extends and straightens	small numbers of melanophores in epidermis of dorsal surface and around lens	37	less prominent	38	28	XXVIII
36 (Fig. 9B)	rectum begins to develop and operculum appears	dorsal fin ⅓ of length of trunk	more melanophores	39	no longer prominent externally	39	—	XXIX
37 (Fig. 10A, Plate 3A)	developing upper lip involves nerves, 'platelet' stage of endoderm cells second cleft covered	dorsal fin ½ of length of trunk small ventral post-anal fin	melanophores spread ventrally	39		—	30	XXXI
38 (Fig. 10B)	operculum covers 3rd cleft, mouth cavity deeper, lower lip starts to form	dorsal fin reaches back of head, post-anal ventral fin grows, small pre-anal ventral fin appears	melanophores increase			41	—	XXXII
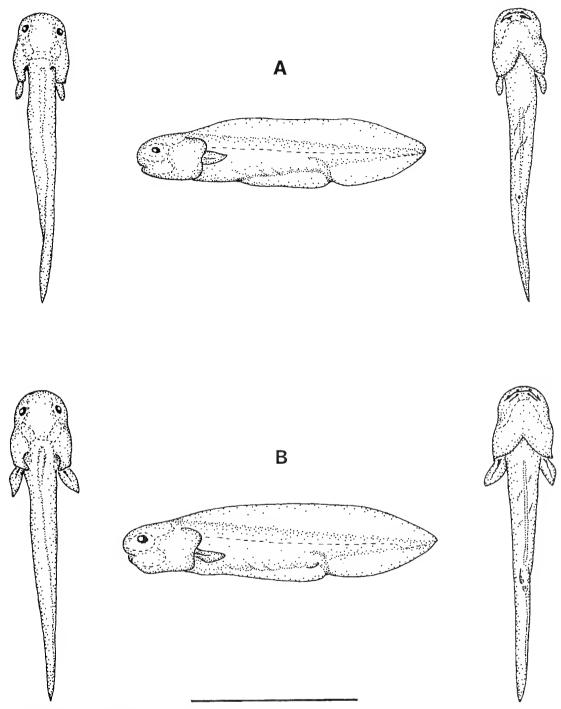
FIG. 14. Drawings of fixed fish showing the appearance of the spiral valve and of the pelvic fin. Dorsal view on the left, lateral in the centre, and ventral on the right. A, stage 47, in which the spiral valve shows clearly as the last of the yolk disappears, the skeleton of the pectoral fin shows through the skin, the sensory lines break up into a series of pits and the supratemporal cross commissure appears; B, stage 48, in which the primordium of the pelvic fin appears in lake eggs, gular pits are well-formed and the pre-anal ventral fin reaches the level of the opercular folds in the mid-ventral line. s. — spiral valve. Scale line = 1 cm.

TABLE 8: Characteristics of Stage 39–43

Stage	External Features	Medial Fins	Paired Fins	Chromatophores	Lateral Line	Stage (Semon 1893)	Stage (Kerr 1909) L. paradoxa	Stage (Kerr 1909) P. annectens
39 (Fig. 11A)	endoderm cells packed into blocks, operculum larger			melanophores increase		42	31	—
40 (Fig. 11B)	operculum covers 4 slits, lower lip distinct	dorsal and ventral fins grow		melanophores increase		43	—	XXXIV
41 (Fig. 12A)	operculum covers all posterior gill slits, mouth cavity joins foregut, lower lip grows forwards			melanophores increase	lateral line of body ⅓ way along trunk	—	—	—
42 (Fig. 12B, Plate 3B)		pre-anal fin grows forward mid-ventrally	Primordium of pectoral fin appears behind operculum	melanophores increase	lateral line of body ⅓ way along trunk	44	32	XXXV
43 (Fig. 12C)	opercular folds almost meet midventrally; yolk content of cells reduced		pectoral fin grows, has pigment cells	red chromatophores present dorsally	lateral line almost reaches tail tip	—	—	—
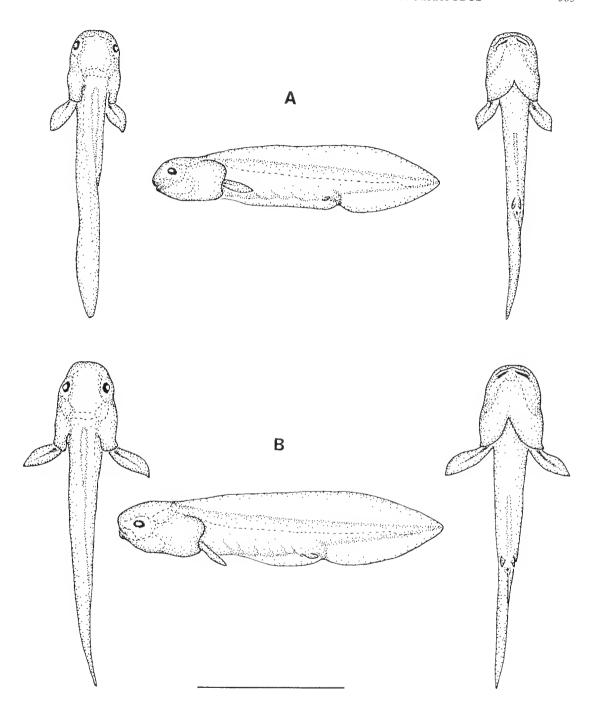
FIG. 15. Drawings of fixed fish showing the regression of the pre-anal ventral fin and growth of the pelvic fins. Dorsal view on the left, lateral in the centre, and ventral on the right. A, stage 49, with an additional line of sensory pits, the oral line, running along the lower lip, some regression in the ventral pre-anal fin and growth of the pelvic fin; B, stage 50, showing further regression of the pre-anal ventral fin and extension of the paired fins. Scale line = 1 cm.

TABLE 9: Characteristics of Stage 44–49

Stage	Gut	Medial Fins	Paired Fins	Chromatophores	Lateral Line System	Stage (Semon 1893)	Stage (Kerr 1909) L. paradoxa	P. annectens
44 (Fig. 13A, Plate 3C)	quantity of yolk in endoderm cells reduced, lower lip grows forwards and almost meets upper lip, anterior shift of mouth starts, nares are visible within upper lip, opercular folds meet in mid-ventral line	pre-anal fin extends half way along yolky cell mass	pectoral fin grows	many pigment cells of both types; animal changes colour according to light	head lines indicated body line bends slightly just before reaching tail	45	—	—
45 (Fig. 13B)	lower lip meets upper		pectoral fin partly covered by operculum	many pigment cells of both types; animal changes colour according to light	in side view, temporal, supra- and infra-orbital and body lines are present; in dorsal view temporal and posterior head lines, and in ventral view the mandibular line	46		

TABLE 9: (Continued)

| Stage	Gut	Medial Fins	Paired Fins	Chromatophores	Lateral Line System	Stage (Semon 1893)	Stage (Kerr 1909) L. paradoxa	P. annectens
46 (Fig. 13C)	mouth shifts further anteriorly, indications of gular pits in lower lip	pre-anal fin extends further forwards		many pigment cells of both types; animal changes colour according to light	jugal line present	—	34	—
47 (Fig 14A, Plate 3D)	yolk in endoderm cells sufficiently reduced to show spiral valve of gut, gular pits develop on either side of lower lip		axial skeleton of pectoral fin appears	many pigment cells of both types; animal changes colour according to light	supra-temporal cross commissure appears, lines break up into pits	—	—	—
48 (Fig. 14B, Plate 3E)	yolk reduced, spiral valve well developed	pre-anal fin reaches back of opercular folds	primordium of pelvic fin appears anterior to anus	many pigment cells of both types; animal changes colour according to light		47	35	—
49 (Fig. 15A, Plate 3F)	yolk gone	pre-anal fin starts to regress, fin rays present in dorsal and post-anal ventral fin	pectoral fin large, mostly free of operculum, pelvic fin has pigment cells	many pigment cells of both types; animal changes colour according to light	oral line present	—	—	XXXVI
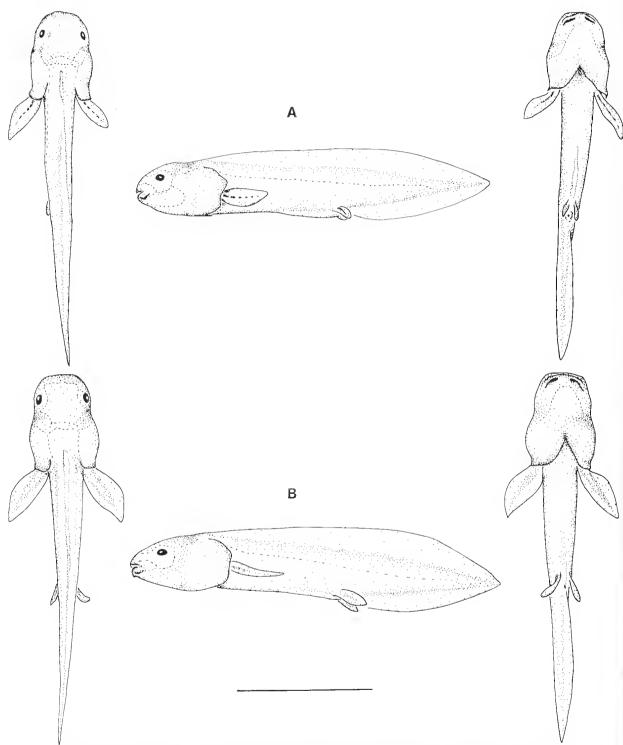
FIG. 16. Drawings of fixed fish. Dorsal on the left, lateral in the centre, and ventral on the right. A, stage 51, with a broad head, narrow body, nearly terminal mouth and showing regression of the ventral pre-anal fin; B, stage 52, the ventral pre-anal fin is almost gone and the head and paired fins are large in relation to the body. The mouth is terminal at this stage. Scale line = 1 cm.

TABLE 10: CHARACTERISTICS OF STAGES 50–55

Stage	External Features	Mouth	Nares	Medial Fins	Paired Fins	Chromatophores	Lateral Line System
50 (Fig. 15B)	head broad, body narrow (cf. stage 48 Semon 1893)		anterior portion of anterior nares show within upper lip	pre-anal fin continues to regress		pigment cells of both types are present all over the body, larva shows marked response to light	as stage 49 but less easy to see
51 (Fig. 16A, Plate 3G)		terminal in position	nares do not show	pre-anal fin extends less than half way to operculm	axial skelton present in pelvic fin	pigment cells of both types are present all over the body, larva shows marked response to light	
52 (Fig. 16B)	scale primordia appear	terminal in position		pre-anal fin nearly gone			
53 (Fig. 17A)	body begins to thicken (cf *L. paradoxa* st. 36, Kerr 1909)			no pre-anal fin	pelvic fin large, both fins used to support body when feeding	pigment cells of both types are present all over the body, larva shows marked response to light	
54 (Fig. 17B)	scales distinct	no longer terminal	in ventral view anterior nares show	medial dorsal fin does not reach head	pelvic fin large, both fins used to support body when feeding	heavily pigmented dorsally, belly pale, red chromatophores not obvious, response to light lost.	hard to distinguish on head
55 (Plate 3H)	scales of adult pattern, body of adult proportions	not terminal, lower jaw narrower than upper, fits within, cf. adult	in ventral view anterior nares show	medial dorsal fin ends mid-dorsally cf. adult	pelvic fin large, both fins used to support body when feeding	spots of intense dark brown pigment appear on the dorsal fin	hard to distinguish on head
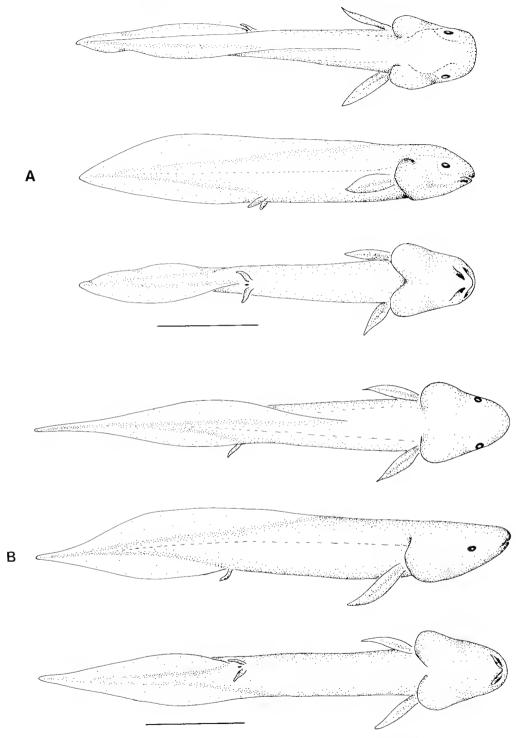
FIG. 17. Drawings of fixed fish showing the gradual assumption of the adult form. Upper is dorsal, lateral in the centre and lower is ventral. A, stage 53, showing thickening body, disappearance of the ventral pre-anal fin and initial regression of the dorsal fin. The mouth is not terminal; B, stage 54, showing body proportions similar to those of the adult, dorsal fin extending forwards as far as the middle of the trunk and the sub-terminal mouth with the anterior nares showing inside the upper lip. Scale line = 1 cm.

PLATE 1.

EGGS AND EMBRYOS OF *NEOCERATODUS FORSTERI*

A,B within the membranes, C–I a sequence of fixed eggs removed
from the membranes showing normal cleavage and blastula formation,
J–L fixed eggs removed from the membranes showing abnormal
cleavage patterns. A, A photograph of the flat surface of a living
uncleaved egg of stage 1 showing the inner membranes, diffuse
pigment, dark spot and pale area; B, a fixed embryo of stage 35
showing the outer albumen membranes, expanded intravitelline space
and the broken inner membranes; C, the flat surface of a normal egg,
prior to first cleavage, without pale area or dark spot and with the
pigment confined to the flat surface; D, a side view of an egg at stage
3 showing the hemispherical shape and cleavage furrows, and the
unequal distribution of pigment and pale area to the cleavage products;
E, the flat surface of an egg at stage 4, showing three cleavage furrows
bisecting the cells produced by the previous division and one furrow
cutting across the cell; F, an egg at stage 5 photographed obliquely
to show part of the side and part of the flat surface; there is no trace
of the pale area and the hemispherical shape is less obvious as the
segmentation cavity expands; G, an egg at stage 7 showing most of
the unpigmented convex surface and some of the pigmented cells of
the previously flat surface; cells of the convex surface are flattened
against the vitelline membrane in the living egg (pavement cells) and
the smaller pigmented cells project into the intravitelline space; H,
a large-celled blastula of stage 8 showing the pigmented region; cell
outlines are indistinct as cell division is in progress; I, a blastula at
stage 9, with pigment confined to the smaller cells; the segmentation
cavity is further enlarged and the hemispherical shape has been
obliterated; J, the convex surface of an egg at stage 2 with pigment
abnormally positioned over one third of the convex surface and an
undivided pale area; K, an egg of normal pigment pattern in which
abnormally positioned cleavage furrows are developing (cf. Semon
1893, stage 5, plate 1 fig. 50); L, flat surface of an egg showing a
common result when first cleavage is latitudinal; the small cell
separated from the larger one divides repeatedly before furrows appear
in the latter. a. — pale area, d. — dark spot, f. — cleavage furrow,
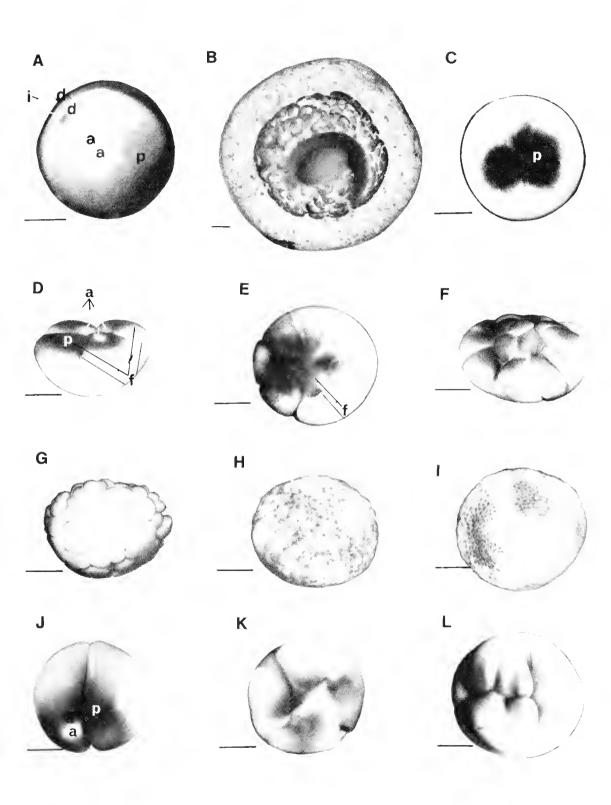i. — inner membrane, p. — pigment. Scale lines = 1 cm.

PLATE 2.
FIXED EGGS AND EMBRYOS OF *N. FORSTERI.*

A, B gastrulae, C–E early neurulae F–J, development of the head. A and B, egg within the membranes, C–J after removal from membranes. A, an egg at stage 12 showing early development of the blastopore; pigmented cells are invaginating over the lip, dragging unpigmented pavement cells inwards; B, a gastrula at stage 15 showing the dorsally constricted blastopore with the lateral lips swinging inwards, and the absence of a ventral lip; C, an embryo of stage 17 showing the dorsoventrally orientated blastopore; D, an embryo of stage 18, looking down on the neural plate, which is slightly raised anteriorly and lined with pigment; E, an embryo of stage 22, looking down on the neural folds, showing the transverse crest (sunk inwards) and the primary brain vesicles; F, a lateral view of an embryo of stage 26, showing the otic vesicle and the head growing out from the rounded mass of yolky cells; G, an embryo of stage 30 looking down on the head and posterior part of the ventral surface (the embryo at this stage is almost circular) showing the developing head, presumptive gill region and anus; H, a lateral view of an embryo of stage 32 showing the rounded endoderm, eye, presumptive gill region, pronephros, axis of body, anus and tail bud; I, a ventral view of an embryo of stage 33 showing nares, mouth region (stomodaeum), endoderm, anus and tail bud; J, a dorsal view of an embryo of stage 35 showing tail bud, lengthening body axis, pronephros, presumptive gill region and hindbrain forming under the skin. a. — anus, b. — blastopore, d. — dorsal lip of blastopore, f. — forebrain, g. — presumptive gill region, h. — hindbrain, l. — lateral lips of blastopore, m. — midbrain, n. — nares, n.f. — neural folds, n.p. — neural plate, o. — otic placode, p. — pigment, pn. — pronephros, s. — stomodaeum, t. — transverse crest, t.b. — tail bud. Scale lines = 1 mm.
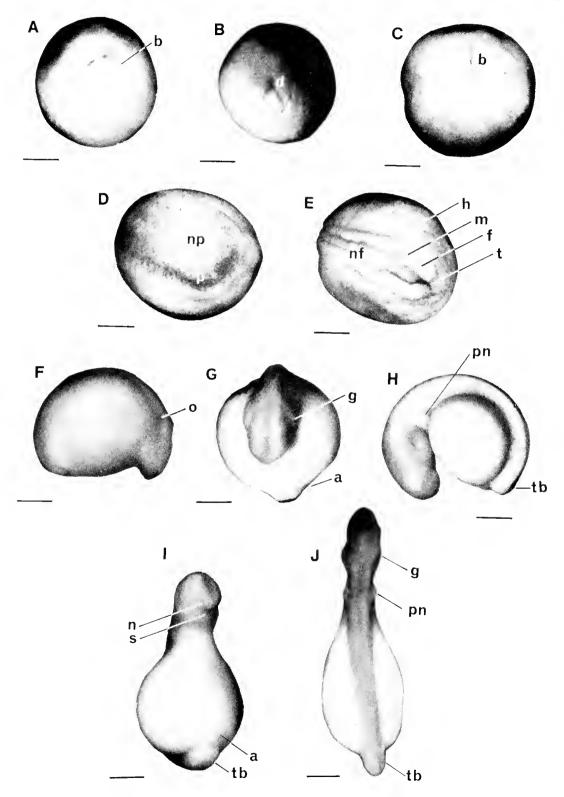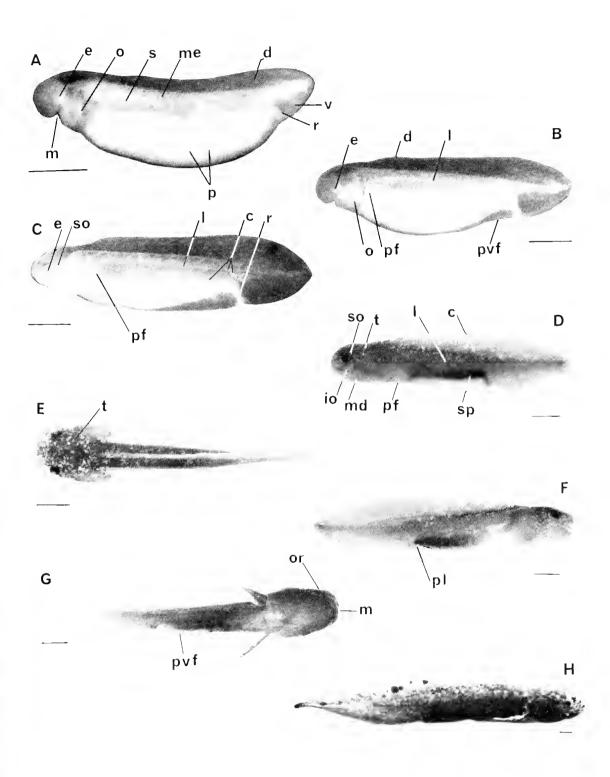
PLATE 3.

EMBRYOS AND JUVENILES OF *N. FORSTERI*

A–C stages prior to hatching, D–H, post-hatching. A, embryo of stage 37 in lateral view showing the platelet arrangement of the endodermal cells, the eye, mouth, primordium of the operculum, somites, melanophores, rectum and the extension of the tail bud, with dorsal and ventral fins; B, lateral view of an embryo of stage 42 showing the extension of the dorsal fin to the back of the head, appearance of the ventral pre-anal fin, the operculum, the eye, the lateral line reaching halfway down the trunk, primordium of the pectoral fin and melanophores covering the whole body; C, animal of stage 44 in lateral view showing the lateral line extending to the tail, the appearance of the supraorbital sensory line of the head, increased growth of all fins, appearance of red chromatophores and development of the operculum and the mouth; D, lateral view of a fish of stage 47 showing remnants of the yolk and traces of the spiral valve in the gut, development of the pectoral fin, mandibular infraorbital, supraorbital and temporal sensory lines and nearly terminal mouth; E, dorsal view of a fish of stage 48 showing the temporal sensory line of the head, pigment in the eye and increase in the melanophores and red chromatophores in the skin; F, fish of stage 49 in lateral view with reduced ventral pre-anal fin and the primordium of the pelvic fin; G, ventral view of a fish of stage 51 showing the developing pectoral fin, sensory line including the oral line broken into a series of pits, skeleton of the pectoral fin, nearly terminal mouth and regression of the pre-anal fin; H, living fish of stage 55 showing pigment spots on the tail and regression of the dorsal fin. d. — dorsal fin, c. — red chromatophores, e. — eye, i.o. — infraorbital sensory line, l. — lateral line, m. — mouth, md. — mandibular sensory line, me. — melanophores, o. — operculum, or. — oral line, p. — platelets of yolky cells, pf. — pectoral fin, pl. — pelvic fin, pvf. — pre-anal ventral fin, r. — rectum, s. — somites, so. — supraorbital sensory line, sp. — spiral valve and yolk remnants, t. — temporal sensory line, v. — ventral fin. Scale lines = 2 mm.

A CATALOGUE OF FOSSIL FISH IN QUEENSLAND

SUSAN TURNER
Queensland Museum

The first one hundred years of palaeoichthyology in Queensland are over and yet the state of the science is still discovery. Very little is known of the fossil fish faunas and very few complete descriptions of those found have been made. There has never been a full-time palaeoichthyologist employed in the state even though fossil fish are of use in stratigraphical correlation and palaeogeographical studies.

This paper is a summary of the present knowledge of fossil fish faunas in Queensland taken principally from the literature. Records are laid out chronologically, with synonymies where possible, after the style of the Fossilium Catalogus. Reference is made to Queensland specimens only, so full synonymies of some species well known outside the state e.g. *Lamna appendiculata*, are not given. In a few cases where only preliminary notice of forms has been made e.g. some placoderms, I have made only a chronological list. Otherwise classification follows various authors e.g. Nelson, 1976; Romer, 1966. This review is probably complete for most species but all references to merely 'fish fragments' or the like in the literature are not necessarily included. To do this would entail a more thorough review of all Geological Survey reports etc. If known to the author, the location of type, figured and other material is given.

My thanks to the Director of the Queensland Museum, Dr Alan Bartholomai; Dr Anne Kemp, Research Fellow, and to Mr. Andrew Rozefelds, Geology Section; and to the librarians of this museum and those of the Geology Dept., University of Queensland, for their help and provision of facilities to carry out this study.

PALAEOZOIC

The first agnathan remains to be found in the Southern Hemisphere were discovered in Queensland (Jones, in Pritchard & Reynolds 1964). These are microvertebrate remains, scales of thelodonts of Early Devonian age (see e.g. Turner et al. 1981). In the last 15 years, study of such microvertebrate remains has become important for biostratigraphical work, especially in the Siluro-Devonian. New material, including thelodonts, acanthodians, sharks, placoderms and bony fishes are now being investigated principally from two areas, the Toko Syncline of the Georgina Basin and the Broken River embayment.

As yet no Silurian or Ordovician fish have been found in the state, whereas the latter are known from the Amadeus Basin, NT (Ritchie & Gilbert-Tomlinson 1977) and might be expected in Queensland.

Upper Palaeozoic faunas are even less well known. Not one proper description of a fauna has been made, and there is doubt about the age of some of the fish-bearing rocks. The Telemon Formation, for example, has been referred to both Upper Devonian and Lower Carboniferous. Detailed study of the fish in these rocks should help to resolve this point. An interesting fauna of bony fishes from the Permian is to be described in the near future by K.S.W. Campbell and Lee Duy Phuoc of ANU, Canberra (Campbell 1981).

DEVONIAN

AGNATHA
THELODONTI
O. THELODONTIDA
F. TURINIIDAE

Turinia cf. *T. pagei* (Powrie, 1870)

1973 *Turinia pagei:* Jones in Turner, p. 573.
1981 *Turinia* cf. *pagei:* Turner et al., p. 54, Figs. 6–8.
1981 *Turinia* cf. *pagei:* Young & Gorter, p. 90.

MATERIAL: scales BMR CPC200979 Loc. GEO 65/28 Toomba Range, Toko Syncline, Georgina Basin.

AGE: Early Devonian, Emsian or older, Cravens Peak Beds.

Turinia australiensis Gross, 1971

1965 coelolepidid scales: Jones in Reynolds and Pritchard.
1965 fish scales: Reynolds, p. 13.
1967 coelolepidids: Johnstone et al., p. 610.
1967 isolepid fish scales: Hill, p. 615.
1968 Coelolepidae: Gilbert-Tomlinson, p. 201.
1972 *Turinia*: Strusz, p. 499.
1973 *Turinia* sp?: Jones in Halstead and Turner, p. 74.
1973 *Turinia pagei* in pars: Turner, p. 573.
1975 fish scales: Talent et al., p. 22.
1981 *Turinia australiensis*: Turner et al., p. 58–59, figs. 9–12.
1981 *Turinia australiensis*: Young & Gorter, p. 90.

MATERIAL: scales BMR CPC20071, 20080–85 Loc. shot point samples, W of Toko Range, Georgina Basin.

AGE: Early Devonian, Emsian or older, Cravens Peak Beds.

F. NIKOLIVIIDAE

Gampsolepis? sp.

1981 *Gampsolepis?* sp. undet.: Turner et al., p. 60, fig. 14.

MATERIAL: scale BMR CPC20086 Loc. GE065/28, Toomba Range, Georgina Basin.

AGE: Early Devonian, Emsian or older, Cravens Peak Beds.

PLACODERMI
O. ANTIARCHI
F. BOTHRIOLEPIDAE?

Bothriolepis? sp.

1936 Antiarch: Hills, p. 163, fig. 3.
1958 *Asterolepis*: Hills, p. 89.
1960 antiarchan fish remains: Hill and Denmead, p. 154.
1962 *Antiarchan*: White, p. 7.
1967 antiarchan fish: Hill, p. 615.
1967 *Asterolepis?*: Hill et al., p. d30, pl. DXV, fig. 1.
1968 *Asterolepis*: Gilbert-Tomlinson, p. 207.
1973 Antiarchan fish remains: Smart, p. 7.
1981 *Bothriolepis?* sp.: Young & Gorter, p. 90.

MATERIAL: median d. plate UQF13909 Loc. Gilberton distr.

AGE: Late Devonian, Gilberton Fm.

O. ARTHRODIRA
F. WUTTAGOONASPIDAE

Wuttagoonaspis sp.

1968 cf. *Coccosteus*: Gilbert-Tomlinson, p. 203.
1973 *Wuttagoonaspis* sp.: Ritchie, p. 70.
1981 *Wuttagoonaspis* sp.: Turner et al., p. 60.
1981 *Wuttagoonaspis* sp.: Young & Gorter, p. 90.

MATERIAL: BMR Loc. Toomba Range incl. GE065/28, Georgina Basin.

AGE: Early Devonian, Emsian or older, Cravens Peak Beds.

Placodermi various

1980 antiarch placoderm, and ? arthrodire: Wyatt & Jell, p. 211.
1981 pterichthyodid antiarch: Turner et al., p. 60; Young & Gorter, p. 90.
1981 phlyctaeniids: Turner et al., p. 60; Young & Gorter, p. 90
1981 large placoderms: Young & Gorter, p. 90.
1981 large brachythoracid: Young & Gorter, p. 90.
1981 antiarchs: Young & Gorter, p. 90.

MATERIAL: BMR, UQF Loc. Toomba Range, Georgina Basin, Burdekin — Star shelf and Broken River embayment. Colls. G.C. Young, J.S. Jell, and D.H. Wyatt.

AGE: L/M/U Devonian, incl. Cravens Peak Beds & Vanneck Fm.

ACANTHODII
O. ISCHNACANTHIDA
F. ISCHNACANTHIDAE

Gomphonchus sp.

1981 *Gomphonchus:* sp.: Turner et al., p. 60, fig. 14A–C.

MATERIAL: scales BMR CPC20087 Loc. GE065/28, Toomba Range, Georgina Basin.

AGE: Early Devonian, Emsian or older, Cravens Peak Beds.

O. CLIMATIIDA
F. CLIMATIIDAE

Nostolepis sp.

1981 *Nostolepis* sp.: Turner et al., p. 60, fig. 14D.

MATERIAL: scale BMR CPC20088 Loc. SP799, west of Toko Syncline.

AGE: Early Devonian, Emsian or older, Cravens Peak Beds.

Acanthodii various

1981 acanthodian spines: Turner et al., p. 60.
1981 acanthodian spines: Young & Gorter, p. 90.

MATERIAL: BMR Loc. Toomba Range, Georgina Basin.

AGE: Early Devonian, Emsian or older, Cravens Peak Beds.

'CROSSOPTERYGII'
O. STRUNIIFORMES (ONYCHODONTIFORMES)

Onychodontid undet.

1981 onychodontid scales: Young & Gorter, p. 90.

MATERIAL: BMR, UQF Loc. Toomba Range, Georgina Basin, also present in Broken River embayment (S.T.).

AGE: L/M. Devonian, incl. Cravens Peak Beds.

Crossopterygian undet.

1967 Crossopterygian dermal plate & dentary: Wyatt & Jell, p. 103.

MATERIAL: GSQ. Loc. nr Payne's Lagoon, Burdekin Basin.

AGE: Upper Devonian, nr base Dotswood Fm.

CARBONIFEROUS
ACANTHODII
O. CLIMATIIDA?
F. GYRACANTHIIDAE

Gyracanthides murrayi Woodward, 1906

1890 spines: Musson in Etheridge, p. 72. (?).
1892 *?Ctenacanthus:* Jack & Etheridge, p. 84. (?).
1892 ichthyodorulite fin spines: Jack & Etheridge, p. 138, 139.
1958 *Gyracanthides* type spine: Hills, p. 91.
1960 *Gyracanthides murrayi:* Hill & Denmead, p. 176.
1972 *Gyracanthides murrayi:* Olgers, p. 42.

MATERIAL: spines QMF6663, GSNSW? GSQ Locs. Bogantungan and Hannam's Gap; Lockington nr Springsure; N. Smithfield shaft, Deep Ck. Gympie distr. Colls incl. C.T. Musson, W.H. Rands, James Smith and A. Bartholomai.

AGE: L. Carboniferous, Star Beds, Ducabrook Fm.

ACTINOPTERYGII
O. PALAEONISCIFORMES

Palaeoniscidae gen. et sp. undet. and various

1890 Palaeoniscid: Etheridge, p. 72.
1891 *Palaeoniscus:* Rands, p. 16.
1892 *?Palaeoniscus:* Jack & Etheridge, p. 136, 296.
*1892 *Palaeoniscus Randsi* Eth. fil. nom. nud.: Jack & Etheridge, p. 186.
1925–30 palaeoniscid: Howchin, p. 170.
1929 palaeoniscid fish scales: Reid.
1930 palaeoniscid fish scales: Reid.
1930 Palaeoniscid fish: Whitehouse, p. 31.
1952 *Elonichthys:* Hills.
1958 Palaeoniscid fish: Hills, p. 91.
1960 palaeoniscids: Hill & Denmead, p. 176, 177.
1964 *Elonichthys?* sp.: Hill & Woods, p. c26, pl. CXIV, figs. 14–15.
1964 *?Elonichthys:* Woods, p. 68.
1964 *Elonichthys:* Veevers et al., p. 15.
1968 rhomboid scales: Gilbert-Tomlinson, p. 207.
1969 fish remains: Mollan et al., p. 13.
1969 Palaeoniscidae: Laseron, p. 117.
1972 palaeoniscid fish: Olgers, p. 42.

MATERIAL: GSNSW? GSQ incl. F8616, & L292 Loc. Bogantungan; rail cut, Hannam's Gap; Lornesleigh Stn; Springsure distr.; Ducabrook Hmstd, SE of Emerald; Mt Wyatt & Ukalunda. Colls. incl. C.T. Musson, W.H. Rands, James Smith.

AGE: L. Carboniferous, Ducabrook Fm., Star Beds; Telemon Fm. (U. Devonian?).

REMARKS: The type specimen of *P. randsi* is thought to be GSQ1522 but, as no description was given, all palaeoniscids have been placed together here.

PERMIAN
BRADYODONTI
F. COCHLIODONTIDAE

Deltodus? australis Etheridge fil., 1892.

*1892 *Deltodus? australis* Etheridge, in Jack & Etheridge, p. 93, 296, pl. 39, fig. 11.
1914?*Deltodus australis:* Chapman, p. 261
1958 *Deltodus australis:* Hills, p. 93.

MATERIAL: tooth plate QMF?, specimen not found. Loc. Rockhampton distr. Coll. de Vis

AGE: Permian, Gympie Series.

ACTINOPTERYGII
O. PALAEONISCIFORMES

Palaeoniscidae gen. et spp. undet.

1981 palaeoniscids: Campbell, p. 41.

MATERIAL: ANU?, QMF Loc. Utah Corp. Blackwater Mine.

AGE: Permian.

1972 fish scales: Exon et al., p. 28.

MATERIAL: scales GSQ Loc. small creek 1.5 km ENE of Alpha Hmstd. S of Alpha.

AGE: Permian, Peawaddy Fm.

Summary Species list

DEVONIAN	Acanthodii undet.
	antiarchs
	brachythoracid
	Bothriolepis? sp.
	Gampsolepis? sp.
	Gomphonchus? sp.
	Nostolepis sp.
	onychodont
	Placodermi undet.
	phlyctaenid
	pterichthyodid
	Turinia australiensis Gross, 1971
	Turinia cf. *T. pagei* (Powrie, 1980)
	Wuttagoonaspis sp.
CARBONIFEROUS	*Elonichthys?*sp.
	Gyracanthides murrayi Woodward, 1906
	Palaeoniscus randsi Etheridge fil., 1892
	Palaeoniscids undet.
PERMIAN	*Deltodus? australis* Etheridge fil, 1892
	Palaeoniscids undet.

MESOZOIC

Our knowledge of these vertebrates in Queensland is somewhat better than that of the Palaeozoic. Even so, most of the work has been restricted to the early Cretaceous Rolling Downs Group of central and northern Queensland. Triassic fishes are described from only one site and no Jurassic fishes have been described to date.

TRIASSIC
DIPNOI
F. CERATODONTIDAE

Dipnoan gen. et sp. undet.

1970 dipnoan tooth plates: Bartholomai & Howie, p. 1063.
1972 dipnoan tooth plates: Howie, p. 51.
1972 lungfish: Warren, p. 279, fig. 1.
1979 lungfishes: Thulborn, p. 340.
1979 dipnoan tooth plates: Bartholomai, p. 225.
1980 tooth plates: Warren, p. 25.
1982 lungfish tooth plates: Turner, p. 545.

MATERIAL: QM Loc. L78 The Crater, Rewan.

AGE: L. Triassic, Arcadia Fm, Rewan Gp.

ACTINOPTERYGII
F. SAURICHTHYIDAE

Saurichthys cf. *S. gigas* (Woodward, 1890)

1982 *Saurichthys* cf. *S. gigas:* Turner, p. 545, pl. 1 A–B.

MATERIAL: portion of skull QMF11942 Loc. The Crater, Rewan

AGE: L. Triassic, Rewan Gp., Arcadia Fm.

Actinopterygian gen. et spp. undet.

1958 fragmentary remains: Hills, p. 94.
1972 actinopterygian scales in coprolites: Howie, p. 51.
1979 actinopterygian fishes: Thulborn, p. 341.
1980 patches of fish scales: Warren, p. 25.
1982 actinopterygian scales: Turner, p. 547.

MATERIAL: QM Loc. L78 The Crater, Rewan.

AGE: L. Triassic, Rewan Gp., Arcadia Fm.

CRETACEOUS

ELASMOBRANCHII
O. HYBODONTIFORMES?
F. HYBODONTIDAE?

Hybodus? incussidens De Vis, 1911

*1911 *Hybodus incussidens:* de Vis, p. 18, pl. 11, fig. 3.
1931 *Hybodus incussidens:* Wade, p. 121, 142.
1958 *Hybodus incussidens:* Hills, p. 99.

MATERIAL: incomplete tooth, QMF12194. Loc. O'Connell Creek, nr Richmond, Coll. F.L. Berney of Wyangaria.

AGE: L. Cretaceous, Albian, Rolling Downs Gp., in 'molluscan conglomerate'.

REMARKS: This tooth probably belongs to a modern shark genus.

Hybodus? sp.

1870 *Hybodus?:* Moore, p. 238, 240.
1892 *Hybodus:* Etheridge & Woodward, p. 2.
1925–30 *Hybodus:* Howchin, p. 317.

MATERIAL: teeth and scales, whereabouts unknown Loc. Wallumbilla, N. of Condamine R.

AGE: L. Cretaceous, Albian, Rolling Downs Gp.

REMARKS: Sent by Rev. W.B. Clarke, with *Lepidotes* (see p. 604), for display at the 1862 Exhibition but delayed at sea. Possibly with Moore's collection at Bristol City Museum (U.K.)

O. GALEIFORMES (LAMNIFORMES)
F. CARCHARIIDAE (ODONTASPIDIDAE)

Carcharias sp.

1967 *Carcharias* sp.: Hill et al., p. k26, pl. KXII, fig. 4.

MATERIAL: tooth QMF2265 Loc. Aramac.

AGE: L. Cretaceous, Albian, Toolebuc Lst?

F. ISURIDAE

'Corax' australis Chapman, 1909

*1909 *Corax australis:* Chapman, p. 435, 1 fig.
1914 *Corax australis:* Chapman, p. 267, fig. 124C.
1925–30 *Corax australis:* Howchin, p. 317.
1931 *Corax:* Wade, p. 121, 144.
1958 *Corax australis:* Hills, p. 99.

MATERIAL: tooth NMVP10974 Loc. Hamilton R., abt 40 mls from Boulia Coll. H.A.C. Webb, pres. G.H. Roche.

AGE: L. Cretaceous, Albain, Rolling Downs Gp.

Lamna appendiculata (Agassiz, 1843)

1885 *Otodus appendiculatus:* Etheridge, p. 8.
1888 *Otodus appendiculatus:* Etheridge, p. 157, 158, pl. 4, fig. 1.
1889 *Otodus appendiculata:* Woodward, p. 393.
1892 *Otodus appendiculatus:* Etheridge & Woodward, p. 2.
1892 *Lamna appendiculata:* Jack & Etheridge, p. 503.
1894 *Lamna appendiculata:* Woodward, p. 144
1909 *Lamna appendiculata:* Chapman, p. 452.
1914 *Lamna appendculata:* Chapman, p. 267.
1925–30 *L. appendiculata:* Howchin, p. 317.
1930 *Lamna:* Whitehouse, p. 37.
1931 *Lamna appendiculata:* Wade, p. 121.
1958 *Lamna appendiculata:* Hills, p. 99.

MATERIAL: tooth GSQ? Loc. Kamilaroy, Leichhardt distr. Coll. R.L. Jack.

AGE: L. Cretaceous, Albian, Rolling Downs Gp.

Lamna daviesi Etheridge fil., 1888

*1888 *Lamna daviesii:* Etheridge jun., p. 159, pl. 4, figs. 2–3.
1889 *Lamna daviesii:* Woodward, p. 410.
1892 *L. daviesii:* Etheridge & Woodward, p. 2.
1892 *Lamna daviesii:* Jack & Etheridge, p. 503.
1894 *L. daviesii:* Woodward. p. 444.
1909 *Lamna daviesii:* Chapman, p. 452.
1914 *Lamna daviesii:* Chapman, p. 267.
1914 *Lamna daviesii:* David, p. 284.
1925–30 *L. daviesii:* Howchin, p. 317.
1931 *Lamna daviesii:* Wade, p. 121.
1958 *L. daviesii:* Hills, p. 99.
1968 *Lamna daviesii:* Hill et al., p. k26, pl. KZ11, fig. 5.

MATERIAL: Holotype QMF1021 Loc. Flinders R., Richmond Downs. Coll. de Vis.

AGE: Cretaceous, Albian, Toolebuc Lst?

Lamna sp.

1892 *Lamna:* Jack & Etheridge, p. 397.
1892 *Otodus:* Jack & Etheridge, p. 404.

MATERIAL: GSQ? Locs. on the Leichhardt R, 9 mls from mouth Gunpowder Ck; at 'Stone Hut' on Rockwood Ck.

AGE: L. Cretaceous, Albian, Rolling Downs Gp.

DIPNOI
F. CERATODONTIDAE

Ceratodus wollastoni Chapman, 1914

1981 *Ceratodus wollastoni:* Kemp & Molnar, p. 212, fig. 6.

MATERIAL: upper toothplate QMF10313 Loc. Winton

AGE: L. Cretaceous

ACTINOPTERYGII
O. ASPIDORHYNCHIFORMES
F. ASPIDORHYNCHIDAE

Aspidorhynchus sp.

1872 *Aspidorhynchus* sp.?: Etheridge, p. 346.
1888 *Aspidorhynchus:* Etheridge, p. 156.
1892 *Aspidorhynchus:* Etheridge & Woodward, p.2.
1892 *Aspidorhynchus* sp.: Jack & Etheridge, p. 412, 504.
1914 *Aspidorhynchus* sp.: David, p. 284.
1925-30 *Aspidorhynchus:* Howchin, p. 318.
1931 *Aspidorhynchus:* Wade, p. 142.
1932 *Aspidorhynchus:* Longman, p. 96.
1958 *Aspidorhynchus:* Hills, p. 99.

MATERIAL: original, probably QMF5663–5 Loc. Hughenden Stn. Coll. R. Daintree.

AGE: L. Cretaceous, Albian, Rolling Downs Gp.

REMARKS: This material may belong to *Belonostomus sweeti* and the two genera may, in fact, be synonymous.

Belonostomus sweeti Eth. fil. & Woodward, 1892.

*1892 *Belonostomus sweeti:* Etheridge jun. & Woodward, p. 3, pl. 1, figs. 1–7.
1892 *Belonostomus sweeti:* Jack & Etheridge, p. 407, 504.
1894 *Belonostomus sweeti:* Woodward, p. 444.
1895 *Belonostomus sweeti:* Woodward, p. 437.
1914 *Belonostomus sweeti:* Chapman, p. 267, fig. 124D.
1914 *Belonostomus sweeti:* David, p. 284.
1925-30 *Belonostomus sweeti:* Howchin, p. 317.
1928 *Belonostomus sweeti:* Wilkins, p. 284.
1929 *Belonostomus sweeti:* Chapman, p. 10.
1931 *Belonostomus sweeti:* Wade, p. 133.
1932 *Belonostomus:* Longman, p. 96.
1958 *Belonostomus sweeti:* Hills, p. 99.
1968 *Belonostomus sweeti:* Hill et al., p. k26, pl. KXII, fig. 3.

MATERIAL: holotype NMVP12988 George Sweet coll. 1889 Loc. Marathon Stn., Flinders R., C. Qld; BMNH P.7539 Geo. Sweet pres. 1895;

GSQ, D.P. Ryan coll. Loc. Hughenden; QMF5660 Loc. Pelican, 30 mls NW of Hughenden.

AGE: L. Cretaceous, Albian, Tambo Fm., Toolebuc Lst. Rolling Downs Gp.

O. SEMIONOTIFORMES
F. SEMIONOTIDAE

Lepidotes sp. (?)

1870 *Lepidotus:* More, p. 238, 240.
1892 *Lepidotus:* Etheridge & Woodward, p. 2.
1925-30 *Lepidotus:* Howchin, p. 318.

MATERIAL: scales, whereabouts unknown Loc. Wallumbilla.

AGE: L. Cretaceous, Albian, Rolling Downs Gp.

TELEOSTEI
O. CLUPEIFORMES
F. ICHTHYODECTIDAE

Cladocyclus? sweeti Woodward, 1894.

*1894 *Cladocyclus sweeti:* Woodward, p. 445, pl. X, figs. 2–6.
1901 *Cladocyclus sweeti:* Woodward, p. 111.
1905 *Cladocyclus sweeti:* Etheridge, p. 7.
1931 *Cladocyclus sweeti:* Wade, p. 142.
1958 *Cladocyclus sweeti:* Hills, p. 99.
1965 *Cladocyclus sweeti:* Bardack, p. 54.

MATERIAL: scales, holotype NMVP15571, also P15572–5. Loc. Marathon Stn., Flinders R. Qld. Coll. George Sweet.

AGE: L. Cretaceous, Rolling Downs Gp?

REMARKS: Bardack (1965) doubts this is *Cladocyclus,* which appears to be restricted to the U. Cretaceous of S. America.

Xiphactinus australis (Woodward, 1894)

*1894 *Portheus australis:* Woodward, p. 444, pl. X, figs. 1, 1a.
1901 *Portheus australis:* Woodward, p. 97.
1905 *Portheus australis:* Etheridge, p. 7–8.
1913 *Portheus australis:* Longman, p. 94.
1914 *Portheus:* Chapman, p. 268.
1925-30 *Portheus:* Howchin, p. 318.
1928 (?) *Portheus australis:* Wilkins, p. 284.
1930 *Portheus:* Whitehouse, p. 37.
1931 *Portheus australis:* Wade, p. 142.
1932 *Portheus:* Longman, p. 96.
1958 *Portheus australis:* Hills, p. 99.
1962 *Xiphactinus:* Bardack, p. 387.

1965 *Xiphactinus australis:* Bardack, p. 10, 54.
1968 *Xiphactinus australis:* Hill et al., p. k26, pl. XXII, fig. 1.
1977 *Xiphactinus:* Patterson & Rosen, p. 89.

MATERIAL: Holotype GSQ F2445 Loc. Gidgery Creek, Clutha Stn., nr Hughenden. Pres. J. Burkitt, 2 specimens QMF, Flinders R., nr Hughenden. coll. S. Dunn; QMF1016, 6 mls NE of Richmond; MCZ 5402, Stewart's Creek, nr Hughenden.

AGE: L. Cretaceous, Albian, Rolling Downs Gp.

Ichthyodectid gen. et sp. indet.

1885 vertebrae of small teleost: Etheridge, p. 8.
1894 Teleostean vertebrae, *Cladocyclus sweeti?:* Woodward, p. 447, pl. X, fig. 7.
1911 chirocentridian: de Vis, p. 11.
1932 unnamed vertebrae: Longman, p. 95.

MATERIAL: 5 caudal vertebrae QMF6139 Loc. Station Ck. Afton Downs.

AGE: L. Cretaceous, Rolling Downs Gp?

REMARKS: Woodward compares them with *Cladocyclus gardneri* but states that vertebrae of this form are met with in *Portheus* and *Ichthyodectes.*

F. PACHYRHIZODONTIDAE

Pachyrhizodus marathonensis (Eth. fil., 1905)

*1905 *Ichthyodectes marathonensis:* Etheridge, p. 8, pls. I, II.
1913 *Ichthyodectes marathonensis:* Longman, p. 94.
1931 *Ichthyodectes marathonensis:* Wade, p. 133.
1932 *Ichthyodectes:* Longman, p. 96.
1958 *Ichthyodectes marathonensis:* Hills, p. 99.
1962 *Pachyrhizodus marathonensis:* Bardack, p. 387, fig. 1.
1965 *Pachyrhizodus:* Bardack, p. 10.
1968 *Pachyrhizodus marathonensis:* Hill et al., p. k26, pl. KXII, fig. 2.
1969 *Pachyrhizodus marathonensis:* Bartholomai, p. 249–63, figs. 46–9, pls. 14, 15.
1977 *Pachyrhizodus marathonensis:* Forey, p. 178, fig. 33.

MATERIAL: original now in AM, Plastotype AM cast L504 (also AMNH cast 7940) Loc. Flinders R., nr Marathon Stn. Coll. P.G. Black; QMF355 Flinders R., nr Hughenden; QMF3349 14 mls N of Springvale Stn., SE of

Boulia; QMF5705, F5687-90, & UQF10210 Boree Park Stn., nr Richmond; QMF5691 Sylvania Stn., nr Hughenden; QMF5692 Dinga Ding Stn., nr McKinlay; BMNH P55858.

AGE: L. Cretaceous, Albian, Rolling Downs Gp, Toolebuc Lst.

O. ELOPIFORMES
F. ELOPIDAE?

Flindersichthys denmeadi Longman, 1932.

*1932 *Flindersichthys denmeadi:* Longman, p. 89, figs. 1–3, pls X–XI, figs. 1–3.
1958 *Flindersichthys denmeadi:* Hills, p. 99.
1962 *Flindersichthys denmeadi:* Bardack, p. 388.

MATERIAL: Holotype QMF2210, pres. H.W. Denmead 1931 Loc. 1 ml E of Richmond on Flinders R.; QMF986(?) vertebrae, Robert Poole, Alderley.

AGE: L. Cretaceous, U. Albian, Tambo Series.

SUP. O. ACANTHOPTERYGII

Acanthopterygian gen. et sp. indet.

1911 Acanthoperygian vertebrae: de Vis, p. 11.

MATERIAL: QMF? 4 abdominal vertebrae Coll. F.L. Berney of Wyangaria.

AGE: L. Cretaceous

Fish remains indet.

1870 small teeth of fishes: Moore, p. 234.
1870 enamelled spine-like bodies: Moore, p. 238.
1892 vertebrae teleostean: Jack & Etheridge, p. 397.
1909 indet. fish remains: Chapman, p. 452.
1960 fish remains: Hill & Denmead, p. 323.
1976 fish, ganoid scales: Day, pp. 138, 143.

MATERIAL: Loc. Wallumbilla (whereabouts unknown); NMV, Hamilton R., 40 mls from Boulia, coll. H.A.C. Webb; also probably in GSQ (1892) Kamilaroy; N of Roma, Mt. Lonsdale Hmstd & Burgagary Creek.

AGE: L. Cretaceous, Rolling Downs Gp, incl. Toolebuc Lst Member, also Doncaster & Minmi Members.

Summary Species list

TRIASSIC actinopterygians undet.
Ceratodus sp?
Saurichthys sp. cf. *S. gigas* (Woodward, 1890)

CRETACEOUS acanthopterygian indet.
Aspidorhynchus?
Belonostomus sweeti Eth. & Woodward, 1892
Carcharias sp.
Ceratodus wollastoni Chapman, 1914
Cladocyclus sweeti Woodward, 1894
Corax australis Chapman 1909
Flindersichthys denmeadi Longman, 1932
Hybodus? sp.
Hybodus? incussidens de Vis, 1911
ichthyodectid indet.
Lamna appendiculata Ag., 1834
Lamna daviesi Eth., 1888
Lamna sp.
Lepidotes sp?
Pachyrhizodus marathonensis (Eth., 1905)
Xiphactinus australis (Woodward, 1894)

CAENOZOIC

The scientific literature on Tertiary fishes in Queensland was written almost exclusively by E. Sherborn Hills. However new work is being undertaken and there are several localities with fish material to be described. As in the Palaeozoic so in the Tertiary the study of microvertebrate remains has become important in recent years and such aspects as scale details and otoliths can be employed in stratigraphical work. The need for a good comparative collection of modern bony fish material is being met by the Queensland Museum.

DIPNOI
F. CERATODONTIDAE

Neoceratodus palmeri (Krefft, 1874)
?=*N. forsteri* (Krefft, 1870)

*1874 *Ceratodus palmeri*: Krefft, p. 292 or 293.
1884 *Ceratodus forsteri*: de Vis, p. 43, 2 pls.
1891 *Ceratodus forsteri*: Woodward, p. 274.
1892 *Ceratodus forsteri*: Jack & Etheridge, p. 635, 638, 647, 740.
1928 *Epiceratodus forsteri*: Longman, p. 170.

1928 *Epiceratodus palmeri?*: Longman, p. 171.
1940 *Neoceratodus*: Whitehouse, p. 24.
1958 *E. palmeri*: Hills, p. 103.
1960 *Neoceratodus*: Hill & Denmead, p. 393.
1970 *Neoceratodus forsteri*: Hill et al., p. cz14, pl. CzVII, fig. 4.
1981 *Ceratodus palmeri*: Kemp & Molnar, p. 211, figs. 2–3.

MATERIAL: original dental plate MF10537, also F1146–7, F10540 Loc. Darling Downs; QMF6564 3 mls SE of Chinchilla, Museum Colls 1883; QMF1148, 70 ft down well, Eight Mile Plains; Gregory R, Riversleigh.

AGE: Early Miocene? Pliocene — Recent, incl. Chinchilla Sand & Carl Creek Lst.

REMARKS: Dr. A. Kemp is currently studying these two forms which may be separate species.

Neoceratodus denticulatus (Hills, 1934)

1932 *Epiceratodus*: David, table 1.
*1934 *Epiceratodus denticulatus*: Hills, p. 157, figs. 1–2.
1943 *Epiceratodus*: Hills, p. 95.
1958 *E. denticulatus*: Hills, p. 103.
1960 *Epiceratodus*: Hill & Denmead, p. 346.

MATERIAL: 5 specimens, holotype QMF2347 Loc. Redbank Plains.

AGE: U. Eocene/Oligocene?, Redbank Plains Series, concretionary limonitic mudst.

REMARKS: Dr. A. Kemp after studying comparative material from S. Australia, believes that *N. denticulatus* is synonymous with *N. gregorii* (Anne Kemp, pers. comm. 1981).

'*Epiceratodus*'

1943 *Epiceratodus* sp.: Hills, p. 96, pl. IX, fig. 1.
1958 *Epiceratodus* sp.: Hills, p. 103.
1960 *Epiceratodus*: Hill & Denmead, p. 353.

MATERIAL: 'scale' GSQF1971 Loc. Bore 3, Munduran, The Narrows, Gladstone

AGE: Miocene?

REMARKS: Both Dr. Kemp and myself agree that this identification is suspect and that the 'scale' may be plant remains.

TELEOSTEI
F. OSTEOGLOSSIDAE

Phareoides queenslandicus (Hills, 1934)

*1934 *Phareodus queenslandicus:* Hills, p. 160, pls. XVII–XIX, figs. 3–7.
1943 Osteoglossid: Hills, p. 95.
1958 *Phareodus queenslandicus:* Hills, p. 100.
1960 *Phareodus:* Hill & Denmead, p. 346.
1970 *Phareodus queenslandicus:* Hill et al., p. cz14, pl. CzVII, fig. 2.
1973 *Phareoides queenslandicus:* Taverne, p. 497.

MATERIAL: 13 specimens, holotype QMF2357, also QMF2358-9, F2917, also GSQF1960 and UQF14960 Loc. Redbank Plains, and Cooper's Plains? Coll. F.W. Whitehouse.

AGE: U. Eocene/Oligocene?, Redbank Plains Series.

Scleropages aff. *leichardti* Gunther

1943 *Scleropages* aff. *leichardti:* Hills, p. 96, pl. IX, fig. 2.
1958 *Scleropages:* Hills, p. 101.
1960 *Scleropages:* Hill & Denmead, p. 346.

MATERIAL: operculum GSQF1969 Loc. Bore 1, Munduran, The Narrows, Gladstone.

AGE: Miocene/Oligocene?

F. GONORHYNCHIDAE

Notogoneus parvus Hills, 1934.

*1934 *Notogoneus parvus:* Hills, p. 164, pl. XX, figs. 8–9.
1958 *Notogoneus parvus:* Hills, p. 100.
1960 *Notogoneus:* Hill & Denmead, p. 346.
1970 *Notogoneus parvus:* Hill et al., p. cz14, pl. CZVII, fig. 3.

MATERIAL: 5 specimens, holotype QMF2364 also QMF2362, 63, 65. Loc. Redbank Plains Coll. F.W. Whitehouse.

AGE: U. Eocene/Oligocene?, Redbank Plains Series.

F. PLOTOSIDAE

Tandanus sp.

1929 *Tandanus* sp. cf. *tandanus:* Longman, p. 249.

MATERIAL: ant. d. spine cf. recent 'Dewfish' QMF2120 Loc. Brigalow, Darling Downs Coll. Zeller Bros., 1929 well sinking; QMF1180 Chinchilla.

AGE: Pleistocene?

REMARKS: Woods (in Hill & Denmead 1960, p. 394) mentions 3 species of fish from Fluviatile (Pleistocene?) deposits but does not elaborate.

F. PERCICHTHYIDAE (Moronidae)

Maccullochella macquariensis (?)

1929 *Oligorus* sp.: Longman, p. 249
1929 *Oligorus macquariensis:* Longman, p. 249.

MATERIAL: ant. d. spine QMF2122 Loc. Brigalow, Darling Downs Coll. Zeller Bros., 1929 well sinking: QM old collections Darling Downs.

AGE: Pleistocene?

REMARKS: This species may be the same as the Recent Murray Cod.

'Percalates' antiquus Hills, 1934

*1934 *Percalates antiquus:* Hills, p. 166, pls. XXI–XXIV, figs. 10–13.
1943 *Percalates:* Hills, p. 95.
1959 *Percalates antiquus:* Hills, p. 100
1960 *Percalates:* Hill & Denmead, p. 346.

MATERIAL: 19 specimens, holotype QMF2370 also QMF2366, F2374–2380, Loc. Redbank Plains Coll. F.W. Whitehouse.

AGE: U. Eocene/Oligocene?, Redbank Plains Series.

REMARKS: The generic status is uncertain: modern species of *Percalates* are now referred to *Macquaria.*

'Percalates' sp.

1970 *Percalates* sp.: Hill et al., p. cz14, pl. CZVII, fig. 1.

MATERIAL: QMF6565 Loc. Brittain's Q., Darra.

AGE: L. Tertiary, Darra Fm.

'Percalates' sp.

1943 *Percalates* sp.: Hills p. 97, pl. IX, fig. 4.
1958 *Percalates:* Hills, p. 101.
1960 *Percalates:* Hill & Denmead, p. 353.

MATERIAL: 2 scales GSQF1968 Loc. Bore 1, Munduran, The Narrows, Gladstone.

AGE: Miocene? (Oligocene?)

'Percalates'? sp.

1934 *Percalates* (?) Ramsay and Ogilby 1887: Hills, p. 168.

MATERIAL: fragmentary remains QM? or GSQ Loc. W. of Strathpine, and E of Bald Hills nr edge Bald Hills Basin Coll. L.C. Ball.

AGE: Oligocene?, oil shales.

'Percalates'?

1934 Genus indet./young *Percalates*?: Hills, p. 169. pl. XXV, fig. 14.

MATERIAL: half small fish GSQF1961 Loc. well, Portion 122, Parish of Bundamba. Coll. F.W. Whitehouse.

AGE: Oligocene?

Percoid indet.

1943 Indeterminate Percoid fish: Hills, p. 97, pl. IX, fig. 5.

MATERIAL: scale GSQF1974 Loc. Parish of Wallbury; GSQF1970 220 ft, Bore 3, Munduran, The Narrows, Gladstone; GSQF1973 256 ft, Bore 3, Munduran.

AGE: Miocene? (Oligocene?)

F. THERAPONIDAE

Theraponid gen et sp. undet.

1981 theraponid: Turner, p. 40.

MATERIAL: otolith QMF12060 Loc. Rundle, E. Qld.

AGE: Oligocene?, Rundle Oil Shale Fm.

REMARKS: Identified by Dr R. Mackay.

F. LUTJANIDAE

Lutjanus sp. cf. *L. erythropterus* Bloch

1943 *Lutjanus* sp.: Hills, p. 97, pl. IX, fig. 3.
1958 (?)*Lutianus*: Hills, p. 101.
1960 *Lutjanus*: Hill & Denmead, p. 353.

MATERIAL: preoperculum GSQF1967 Loc. Bore 1, Munduran, The Narrows, Gladstone.

AGE: Miocene?

REMARKS: Hills (1943) states this form to be comparable though larger than the Recent *L. erythropterus*.

Teleost Order indet.

1934 Order indet.: Hills, p. 170.

MATERIAL: fragments axial skeleton and fin spines QM? Loc. Redbank Plains.

AGE: U. Eocene/Oligocene?, Redbank Plains Series.

Fish Remains Indet.

1900 fish remains: Dunstan, p. 16-17.
1901 fish remains: Dunstan, p. 20.
1916 fish remains: Dunstan, p. 9.
1934 fish remains: Hills, p. 155.
1943 fish remains: Hills, p. 95.
1960 fish: Hill & Denmead, p. 354.

MATERIAL: GSQ? Locs. between NW of Duaringa and Wallaroo; Darra.

AGE: L. Tertiary, Duaringa shales; Darra Fm.

REMARKS: Hills (1934) states that Dunstan's material was 'no longer available'.

SUMMARY SPECIES LIST

EOCENE/ OLIGOCENE	*Neoceratodus denticulatus* (Hills, 1934)
	Notogoneus parvus Hills, 1934
	Order indet.
	Phareoides queenslandicus (Hills, 1934)
	'Percalates' antiquus Hills, 1934
	'Percalates' sp.
	'Percalates'? sp.
	theraponid
MIOCENE	*Lutjanus* sp.
	Neoceratodus sp.
	'Percalates' sp.
	percoid
	Scleropages aff. *S. leichardti*
PLIOCENE/ PLEISTOCENE	*Maccullochella macquariensis*?
	Neoceratodus forsteri (Krefft, 1870)
	Neoceratodus palmeri (Krefft, 1874)
	Tandanus sp.

Abbreviations

Fossil collections: AM – Australian Museum, AMNH – American Museum of Natural History, ANU – Australian National University Geology Dept., BMNH – British Museum (Natural History), BMR – Bureau of Mineral Resources, GSNSW – Geological Survey New South Wales, GSQ – Geological Survey Queensland, MCZ –

Museum of Comparative Zoology, NMV – National Museum of Victoria, QM – Queensland Museum, UQ – University of Queensland Geology Dept.

abt – about, ant. – anterior, Ck – creek, Coll. – collector, d. – dorsal, distr. – district, Fm – Formation, ft – feet, Gp. – Group, Hmstd – homestead, incl. – including, L. – Lower, Loc. – locality, mls. – miles, nr – near, Pres. – presenter, Q. – quarry, R. – river, Stn. – station, U. – Upper, * denotes new taxon.

LITERATURE CITED

BARDACK, D., 1962. Taxonomic status and geological position of the Cretaceous fish *Ichthyodectes marathonensis. Aust. J. Sci.* 24: 387–8.

1965. Anatomy and Evolution of Chirocentrid Fishes. *Univ. Kansas Paleont. Contribs., Vertebrata* 10: 1–88.

BARTHOLOMAI, A., 1969. The Lower Cretaceous Elopoid Fish *Pachyrhizodus marathonensis* (Etheridge Jnr.). *In* 'Stratigraphy and Palaeontology. Essays in honour of Dorothy Hill.' Ed. K.S.W. Campbell, (Canberra: A.N.U. Press) 249–63.

1979. New lizard-like reptiles from the Early Triassic of Queensland. *Alcheringa* 3: 225–34.

BARTHOLOMAI, A. and A. HOWIE, 1970. Vertebrate fauna from the Lower Trias of Australia. *Nature* 225 (5237): 1063.

CAMPBELL, K.S.W., 1981. Report from A.N.U. *Nomen Nudum* 10: 41.

CHAPMAN, F., 1909. On the Occurrence of the Selachian Genus *Corax* in the Lower Cretaceous of Queensland. *Proc. Roy. Soc. Victoria* 21 (N.S.): 452–53.

1914. 'Australasian Fossils. A Student's Manual of Palaeontology.' (Melbourne: Geo. Robertson & Co.) 1–341.

1929. 'Illustrated Guide to the Collection of Fossils exhibited in the National Museum of Victoria.' (Melbourne: H.J. Green) 1–55.

DAVID, T.W.E., 1914. Geology of the Commonwealth. *In* 'Federal Handbook of Australia.' (Melbourne: Government Printer). 241–325.

1932. Explanatory Notes to Accompany a new Geological Map of the Commonwealth of Australia. (Sydney: Austr. Medical Pub. Co.) 1–177.

DAY, R.W., 1976. Aptian and Albian macrofossils from the Mitchell and Roma 1:250,000 sheet areas. Appendix 1. *Bull. Bur. Min. Resour. Geol. Geophys.* 166: 137–50.

DENISON, R.H., 1978. 'Placodermi.' Handbook of Paleoichthyology 5 (Stuttgart: Gustav Fischer Vg) i–vi, 1–128.

1979. 'Acanthodii.' Handbook of Paleoichthyology 2 (Stuttgart: Gustav Fischer Vg) i–vi, 1–62.

DE VIS, C.W., 1884. *Ceratodus Forsteri,* Post-Pliocene. *Proc. Roy. Soc. Qd* 1: 40–43.

1909. On Some Mesozoic Fossils. *Anns Qd Mus.* 10: 1–11.

DUNSTAN, B., 1900. Notes on Fossil Fish at Duaringa, Central Railway Line. *Geol. Surv. Qd Ann. Prog. Rep.* 1900: 16–17.

1901. Geology of the Dawson and Mackenzie Rivers, etc. *Qd Geol. Surv. Pub.* 155: 1–28.

1916. Stratigraphical Features. *In* Tillyard's 'Mesozoic and Tertiary Insects of Queensland and New South Wales.' *Qd Geol. Surv. Pub.* 253: 1–10.

ETHERIDGE, R., 1872. Description of the Palaeozoic and Mesozoic Fossils of Queensland. *Quart. J. Geol. Soc.* 28: 317–50.

ETHERIDGE, R., fil., 1885. Appendix to R.L. Jack's Reports on the Geological Features of parts of the District to be transversed by the proposed Trans-Continental Railway. *Qd Parl. Papers* 1885: 22.

1888. Descriptions of fish remains from the Rolling Downs Formation of Northern Queensland. *Proc. Linn. Soc. N.S.W. (2)* 3: 156–61.

1890. Note on the Occurrence of Fish-remains in the Rocks of the Drummond Range, Central Queensland. *Rec. Geol. Surv. N.S.W.* II: 71–2.

1905. Description of the mutilated cranium of a large fish from the Lower Cretaceous of Queensland. *Rec. Aust. Mus.* 6: 5–8.

ETHERIDGE, R., fil. and A.S. WOODWARD, 1892. On the occurrence of the genus *Belonostomus* in the Rolling Downs Formation of Central Queensland. *Trans. Roy. Soc. Vict.* 2, 2: 1–7.

EXON, N.F., M.C. GALLOWAY, D.J. CASEY and A.G. KIRKEGAARD, 1972. Geology of the Tambo and Augathella 1:250,000 sheet area. *Bur. Miner. Resour. Aust. Rep.* 143: 1–105.

FOREY, P.L., 1977. The osteology of *Notelops* Woodward, *Rhacolepis* Agassiz, and *Pachyrhizodus* Dixon (Pisces, Teleostei). *Bull. Brit. Mus. (Nat. Hist.), Geol.* 28, 2: 123–204.

GILBERT-TOMLINSON, J., 1968. A new record of *Bothriolepis* in the Northern Territory of Australia. *Bur. Miner. Resour. Aust. Bull* 80–11, (Palaeont. Paps 1965): 191–224.

HALSTEAD, L.B. and S. TURNER, 1973. Silurian and Devonian ostracoderms. In 'Atlas and Palaeobiogeography' ed. A. Hallam (Amsterdam:Elsevier) 67–79.

HILL, D., 1967. Devonian of Eastern Australia. *Int. Symp. Dev. Syst., Calgary,* **1:** 613–30.

HILL, D and A.K. DENMEAD, 1960. The Geology of Queensland. *J. Geol. Soc. Aust.* **7:** 1–474.

HILL, D., G. PLAYFORD and J.T. WOODS, 1967. Devonian Fossils of Queensland. (Brisbane: Qld. Palaeontogr. Soc.) 1–32.

1968. Cretaccous Fossils of Queensland (Brisbane: Qld. Palaeontogr. Soc.) 1–35.

1970. Cainozoic Fossils of Queensland. (Brisbane: Qld. Palaeontogr. Soc.) 1–36.

HILL, D and J.T. WOODS, 1964. Carboniferous Fossils of Queensland (Brisbane: Qld. Palaeontogr. Soc.) 1–32.

HILLS, E.S., 1934. Tertiary freshwater fishes from Southern Queensland. *Mem. Qd Mus.* **10:** 157–74.

1936. Records and Descriptions of some Australian Devonian Fishes. *Proc. Roy. Soc. Vict.* **48** (N.S.), II: 161–71.

1943. Tertiary freshwater fishes and crocodilian remains from Gladstone and Duaringa, Qld. *Mem. Qd Mus.* **12:** 95–100.

1952. In Shell (Qld) Development Pty. Ltd. General report on investigations and operations carried out by the company in the search for oil in Queensland 1940–1961. Unpubl. Rep. Geol. Surv. Qld.

1958. A Brief Review of Australian Fossil Vertebrates. *In* 'Studies on Fossil Vertebrates', ed. T.S. Westoll. (London: Athlone Press) 86–107.

HOWCHIN, W., 1925–30. 'The Building of Australia.' (Adelaide: R.E.E. Rodgers) XI + 1–750.

HOWIE, A.A. 1972. On a Queensland labyrinthodont. In 'Studies in Vertebrate Evolution', eds. K.A. Joysey & T.S. Kemp (Edinburgh: Oliver & Boyd) 50–64.

JACK, R.L. and R. ETHERIDGE, Jnr., 1892. 'The Geology and Palaeontology of Queensland and New Guinea. (Brisbane: Govt. Printer) XXXI + 1–768.

JOHNSTONE, M.H., P.J. JONES, W.J. ROBERTS, J. GILBERT-TOMLINSON, J.J. VEEVERS, and A.T. WELLS, 1967. Devonian of Western and Central Queensland *Int. Symp. Dev. Syst., Calgary* 1: 599–612.

KEMP, A. and R.E. MOLNAR, 1981. *Neoceratodus forsteri* from the Lower Cretaceous of New South Wales, Australia. *J. Paleont.* **55:** 211–7.

KREFFT, G., 1870. Description of a giant amphibian allied to the genus *Lepidosiren* from the Wide Bay district, Queensland. *Proc. Zool. Soc. London,* **1870:** 221–4.

1874. *Ceratodus palmeri. Nature* 9: 293.

LASERON, C. and R.O. BRUNNSCHWEILER, 1969. 'Ancient Australia'. (Sydney: Angus & Robertson) 1–253.

LONGMAN, H.A., 1913. Note on *Portheus australis* A.S. Woodward. *Mem. Qd Mus.* **2:** 94.

1928. Discovery of juvenile lungfishes, with notes on *Epiceratodus. Mem. Qd Mus.* **9:** 160–73.

1929. Palaeontological Notes. Specimens from a well at Brigalow. *Mem. Qd Mus.* **9:** 247–51.

1932. A new Cretaceous fish. *Mem. Qd Mus.* **10:** 89–97.

MOLLAN, R.G., J.M., DICKENS, N.F. EXON, and A.K., KIRKEGAARD, 1969. Geology of Springsure 1:250,000 sheet area. *Bur. Miner. Resour. Rep.* **123:** 1–119.

MOORE, C., 1870. Australian Geology and Palaeontology. *Proc. Quart. J. Geol. Soc.* **25:** 226–61.

NELSON, J.S., 1976. 'Fishes of the World'. (New York: John Wiley & Sons) XIII + 1–416.

OLGERS, F. 1972. Geology of the Drummond Basin, Queensland. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* **132:** 1–72.

PATTERSON, C. and D.E. ROSEN, 1977. Review of Ichthyodectiform and other Mesozoic Fishes and the Theory and Practice of Classifying Fossils. *Bull. Amer. Mus. Nat. Hist.* **158,** 2: 81–172.

RANDS, W.H., 1891. Report on the Cape River Gold Field. By authority, Brisbane.

REID, J.H., 1929. Geology of the Bowen River Coalfield. *Geol. Surv. Qld. Pub.* **276:** 1–107.

1930. The Queensland Upper Palaeozoic succession. *Geol. Surv. Qld. Pub.* **278:** 1–96.

REYNOLDS, M.A., 1965. 1:250,000 Geological Series Explanatory notes, Glenormiston, Qld. sheet SF/54–9: 1–22.

REYNOLDS, M.A. and P.W. PRITCHARD, 1964. The geology of the Glenormiston 1:250,000 sheet area. *Bur. Miner. Resour. Aust. Rec.* **1964/28** (unpubl.).

RITCHIE, A., 1973. *Wuttagoonaspis* gen. nov., an unusual arthrodire from the Devonian of western New South Wales, Australia. *Palaeontgr.* **143A,** 59–72.

RITCHIE, A., and J. GILBERT-TOMLINSON, 1977. First Ordovician vertebrates from the Southern Hemisphere. *Alcheringa* 1: 351–68.

ROMER, A.S., 1966. 'Vertebrate Palaeontology'. 3rd Ed (Chicago: Univ. Chicago Press) 1–468.

SHIRLEY, J., 1899. 'International Catalogue of Scientific Literature'. Queensland Volume. (Brisbane: E. Gregory).

SMART, J., 1973. 1:250,000 Geological Series Explanatory notes, Gilberton, Qld. sheet E/54–16. 2nd Ed.

STRUSZ, D.L., 1972. Correlation of the Lower Devonian Rocks of Australia. *J. Geol. Soc. Aust.* **18**, 4: 427–55.

TALENT, J.A., W.B.D.N. BERRY, A.J. BOUCOT, G.H. PACKHAM, and G.C.O. BISCHOFF, 1978. Correlation of the Silurian rocks of Australia, New Zealand and New Guinea. *Geol. Soc. Am. Spec. Pap.* **150**: 1–108.

TAVERNE, L., 1973. Etablissement d'un genre nouveau, *Phareoides,* pour *Phareodus queenslandicus* Hills, E.S., 1934 (Pisces Osteoglossiformes) du Tertiare d'Australie. *Bull. Soc. Belge Geol. Paleont. Hydrol.* **82**: 497–9.

THULBORN, R.A., 1979. A proterosuchian thecodont from the Rewan Formation of Queensland. *Mem. Qd Mus.* **19**: 331–55.

TURNER, S., 1973. Siluro-Devonian thelodonts from the Welsh Borderland. *J. Geol. Soc. Lond.* **129**: 557–84.

—— 1981. Queensland Museum report. *Bull. Soc. Vert. Paleo.* **122**, June: 39–40.

—— 1981. *Saurichthys* (Pisces, Actinopterygii) from the Early Triassic of Queensland. *Mem. Qd Mus.* **20**: 545–51.

TURNER, S., P.J. JONES and J.J. DRAPER, 1981. Early Devonian thelodonts (Agnatha) from the Toko Syncline, Western Queensland and a review of other Australian discoveries. *Bur. Miner. Resour. Austr. Geol. Geophys. J.* **6**: 51–69.

VEEVERS, J.J., R.G. MOLLAN, F. OLGERS and A.G. KIRKEGAARD, 1964. The Geology of the Emerald 1:250,000 sheet area, Queensland, *Bur. Miner. Resour. Rep.* **68**: 1–71.

WADE, R.T., 1931. The Fossil Fishes of the Australian Mesozoic Rocks. *Proc. Roy. Soc. N.S.W.* **64**: 115–47.

WARREN, A.A., 1972. Triassic Amphibians and Reptiles of Australia in Relation to Gondwanaland. *Aust. Nat. Hist.* **1972**: 279–83.

—— 1980. *Parotosuchus* from the Early Triassic of Queensland and Western Australia. *Alcheringa* **4**: 25–36.

WHITE, D.A., 1962. 1:250,000 Geological Series Explantory notes, Gilberton, Qld. sheet E/54–16.

WHITEHOUSE, R.W., 1930. 'The Geology of Queensland.' Handbook Austr. Assoc. Adv. Sci., (Brisbane: Govt. Printer) 23–39.

—— 1940. Studies on the late geological history of Queensland. *Paps. Geol. Dept. Univ. Ad* **2**, 1: 1–74.

WILKINS, G.H., 1928. 'Undiscovered Australia being an account of an expedition to tropical Australia to collect specimens of the rarer native fauna for the British Museum, 1923–1925.' (London: Ernest Benn Ltd) 1–292.

WOODS, J.T., 1964. Fossil fish remains from two localities in the Emerald sheet area. Appendix 2. *Bur. Miner. Resour. Rep.* **68**: 65.

WOODWARD, A.S., 1889. 'Catalogue of Fossil Fishes Pt. 1.' (London: Brit. Mus (N.H.).

—— 1890. The Fossil Fishes of the Hawkesbury Series at Gosford. *Mem. Geol. Surv. N.S.W., Palaeont.* **4**: 1–55.

—— 1891. 'Catalogue of Fossil Fishes Pt. II'. (London: Brit. Mus. (N.H.)).

—— 1894. On some fish-remains of the genera *Portheus* and *Cladocyclus* from the Rolling Downs Formation (Lower Cretaceous) of Queensland. *Ann. Mag. Nat. Hist.* (6), **14**: 444–47.

—— 1895. 'Catalogue of Fossil Fishes Pt. III. '(London: Brit. Mus (N.H.)).

—— 1901. 'Catalogue of Fossil Fishes Pt. IV. '(London: Brit. Mus..(N.H.)).

WYATT, D.H. and J.S. JELL, 1967. Devonian of the Townsville Hinterland, Queensland, Australia. *Int. Symp. Dev. Syst., Calgary,* **II**: 99–105.

—— 1980. Devonian and Carboniferous stratigraphy of the Northern Tasman orogenic zone in the Townsville Hinterland, North Queensland. *In* 'The Geology and Geophysics of Northeastern Australia', eds, R.A. Henderson & P.J. Stephenson, (Townsville: Geol. Soc. Austr. Qld. Div.) 201–28.

YOUNG, G.C. and J.D. GORTER, 1981. A new fish fauna of Middle Devonian age from the Taemas/Wee Jasper region of New South Wales. *Bull. Bur. Miner. Resour.* **209** (*Palaeont. Paps* 1981): 83–147.

A CATALOGUE OF FOSSIL AMPHIBIANS AND REPTILES IN QUEENSLAND

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In the past few years much new Mesozoic reptile and amphibian material has been uncovered in Queensland. Thus the time is ripe for a bibliographic treatment of fossil reptiles and amphibians in Queensland, before the amount of published literature becomes unwieldly. This paper presents such an attempt laid out in the style of *Fossilium Catalogus*. Synonymies are presented wherever possible, and the bibliographic citations are restricted either to specimens from Queensland, or items directly relevant to specimens from Queensland. I have not chosen to cite all works but have included those in the following six categories: substantive works, i.e. descriptions, revisions, etc.; works with illustrations of Queensland material; works with reconstructions or restorations of Queensland material; early records; citations of material that were vague or incomplete and are here clarified; and, interesting citations. Material identified only to a taxon higher than genus has been included where known to me, but no claim to completeness is made. Indeed I would much appreciate hearing from readers knowing of any such material not here included.

Type descriptions are designated by an asterisk. The material cited is the holotype specimen for nominate species unless otherwise designated. Note that all references to the four Hill, Playford and Woods publications are to plate number and not page number.

Abbreviations:
aff., affinity; AM, Australian Museum, Sydney; BMNH, British Museum (Natural History), London; d., dc; F., family; fig., figure; Fm., formation; Gr., group; ifc., inside front cover; indct., indeterminate; LM. Palaeontolgical Institute, University of Lund, Lund; Ls., limestone; Mem., member; NMV, National Museum of Victoria, Melbourne; No., number; O., order; p., page; pl., plate; QM, Queensland Museum, Brisbane; rt., right; sp., species; Ss., sandstone; T., volume (tome); unident., unidentified; USDG, University of Sydney, Department of Geology, Sydney; v., von; vol., volume.

PALAEOZOIC

Almost no tetrapod material is known from the Palaeozoic of Australia, although hopefully such material may be forthcoming in the future, with further exploration of Permian and Carboniferous beds. The only skeletal material thus far known of Palaeozoic tetrapods is from New South Wales, and consists of two Permian labyrinthodonts, *Bothriceps australis* and *Trucheosaurus major*, now considered synonymous, and a Devonian possible ichthyostegalian, *Metaxygnathus denticulus*.

UPPER PERMIAN

Tracks
   1969   animal tracks, possibly bottom-feeding fish: Malone et al., p. 53, pls. 4–5.
   1972a large amphibian, and possible lepospondyl tracks: Warren, p. 160–2, figs. 1–2.
AGE: Blackwater Gr., Burngrove Fm.
REMARKS: The tracks shown in Warren, fig. 1 and interpreted as a tail trace can also be interpreted as claw drag traces. If Warren is correct in interpreting some of these traces as representing a lepospondyl, it would be as she points out the latest known survivor of that group.

MESOZOIC

Until the mid 1960's Mesozoic tetrapods in Australia were known largely from marine forms, plesiosaurs and ichthyosaurs, and only literally a handful of specimens representing terrestrial forms. The discovery of several Triassic sites in Western Australia, in Tasmania and in Queensland has greatly illuminated our understanding of the faunas of the early Triassic. Jurassic tetrapods are still known from five specimens, all from Queensland. One of these, the latest known surviving labyrinthodont, suggests that much of interest remains to be learned from the Australian Jurassic. More fortunately, the Lower Cretaceous is becoming better understood from the discoveries of dinosaurs in southern Victoria and west and north Queensland. Upper Cretaceous tetrapods

are still rare in Australia, reflecting the paucity of recognized Upper Cretaceous sediments. In addition to those listed from Queensland (probably Upper Cretaceous) there are some marine reptile (ichthyosaur, mosasaur and plesiosaur) remains from Western Australia.

LOWER TRIASSIC

AMPHIBIA
O. TEMNOSPONDYLI
F. BRACHYOPIDAE

Brachyops allos Howie 1971

*1971   *Brachyops allos:* Howie, p. 268–77, figs. 1–3, pls. 14–5.
1972b *Brachyops allos:* Warren, p. 281, fig. (second).
1981a *Brachyops allos:* Warren, p. 278–80, 283–4, 286, figs. 8–9.
1981b *Brachyops allos:* Warren, p. 285–9, fig. 1, pl. 1.

AGE: Rewan Gr., Arcadia Fm.

MATERIAL: Skull and jaws (QM F6572).

F. CHIGUTISAURIDAE

Keratobrachyops australis Warren 1981

*1981   *Keratobrachyops australis:* Warren, p. 273–88, figs. 1–11.

AGE: Rewan Gr., Arcadia Fm.

MATERIAL: Skull and jaws (QM F10115).

F. CAPITOSAURIDAE

Parotosuchus gunganj Warren 1980

*1980   *Parotosuchus gunganj:* Warren, p. 29–32, figs. 3–7.

AGE: Rewan Gr., Arcadia Fm.

MATERIAL: Skull and jaw (QM F10114).

Parotosuchus rewanensis Warren 1980

*1980   *Parotosuchus rewanensis:* Warren, p. 26–9, figs. 1–2, 5.

AGE: Rewan Gr., Arcadia Fm.

MATERIAL: Skull (QM F6571).

F. RHYTIDOSTEIDAE

Deltasaurus? sp.

1972b (?) *Deltasaurus:* Warren, p. 281. (In faunal list only).

AGE: Rewan Gr., Arcadia Fm.

F. INDOBRACHYOPIDAE

Rewana quadricuneata Howie 1972

*1972   *Rewana quadricuneata:* Howie, p. 50–64, figs. 1–6, pl. 1.
1972b *Rewana quadricuneata:* Warren, p. 281.
1979   *Rewana quadricuneata:* Cosgriff & Zawiskie, p. 20–1.
1980c *Rewana:* Molnar, p. 48, fig. 3.

AGE: Rewan Gr., Arcadia Fm.

MATERIAL: Skull, vertebrae and haemal arches, ribs, scapulocoracoid, humerus, radius, ulna, ilium, femur, tibia, fibula, phalanges (QM F6471). Most elements are incomplete.

Unidentified labyrinthodont and thecodont material

1926 Crocodilia: Jensen, p. 144.

AGE: Rewan Gr., Arcadia Fm.

REMARKS: This material (QM F1342) is referable to labyrinthodont amphibians (not further identifiable) and a thecodont (probably *Kalisuchus*).

REPTILIA
O. COTYLOSAURIA
F. PROCOLOPHONIDAE

Procolophonid

1970   ?paliguanid reptiles: Bartholomai & Howie, p. 1063, fig. 2.
1975   ?*Procolophon:* Colbert & Kitching, p. 22.
1979   procolophonid: Bartholomai, p. 225.
1980c procolophonian: Molnar, p. 48.

AGE: Rewan Gr., Arcadia Fm.

MATERIAL: Skulls and jaws.

REMARKS: This material is now recognized as pertaining to a procolophonid similar to *Procolophon.*

O. Squamata
F. Paliguanidae

Kudnu mackinlayi Bartholomai 1979

*1979 Kudnu mackinlayi: Bartholomai, p. 231–3, figs. 5–6.
1980c Kudnu mackinlayi: Molnar, p. 48, fig. 4.

Age: Rewan Gr., Arcadia Fm.

Material: Anterior portion of skull and jaws (QM F9181).

F. Prolacertidae

Kadimakara australiensis Bartholomai 1979

*1979 Kadimakara australiensis: Bartholomai, p. 226–31, figs. 1–4.
1980c Kadimakara australiensis: Molnar, p. 48, fig. 5.

Age: Rewan Gr., Arcadia Fm.

Material: Posterior portion of skull and jaw (QM F6710).

O. Thecodontia
F. Proterosuchidae

Kalisuchus rewanensis Thulborn, 1979

*1979 Kalisuchus rewanensis: Thulborn, p. 331–44, fig. 1, pls. 1–5.
1980c Kalisuchus rewanensis: Molnar, p. 48–9.
1980 Kalisuchus rewanensis: Thulborn, p. 246, fig. 5.

Age: Rewan Gr., Arcadia Fm.

Material: Rt. maxilla (QM F8998). Referred material includes other portions of the skull as well as jaws, fore and hind limbs and girdles, and vertebrae.

UPPER TRIASSIC

O. Saurischia
F. Anchisauridae

Agrosaurus macgillivrayi Seeley 1891

*1891 Agrosaurus macgillivrayi: Seeley, p. 164–5, figs. 1–6.
1906 Thecodontosaurus macgillivrayi: v. Huene, p. 50–2, figs. 86–90.
1932 Agrosaurus macgillivrayi: v. Huene, p. 52, 295. (Bibliographic entry only on 295).
1950 Agrosaurus macgillivrayi: David, p. 468.

1955 Agrosaurus: d. Lapparent & Lavocat, p. 800–1.
1956 Agrosaurus: v. Huene, p. 477.
1970 Agrosaurus macgillivrayi: Steel, p. 13.
1976 Thecodontosaurus macgillivrayi: Galton & Cluver, p. 142–3, figs. 11H–J.
1980c Agrosaurus macgillivrayi: Molnar, p. 49–50, fig. 7.

Age: Not known, but presumed Upper Triassic, although such beds are not presently mapped along the northeast Queensland coast where the material was allegedly collected. David has suggested that the material may actually be Lower Jurassic in age.

Material: Tooth, radius, tibia, phalanx (BMNH 49984). A cast of the tibia (QM F11614) is held at the QM.

Tracks

Labyrinthodont tracks

1954 quadruped: Colliver, p. 78–9.
1965 stereospondyl footprint: Hill, Playford and Woods, pl. T13(7)
1966a labyrinthodont amphibian tracks: Bartholomai p. 149.
1973 amphibia and a bipedal animal: Stevens, p. 12.

Age: Tingalpa Fm (at Petrie's Quarry, Albion, Brisbane).

Theropod tracks

1964 probably large bipedal theropod: Staines & Woods, p. 55, fig. 1.
1965 theropod footprint: Hill, Playford & Woods, pl. T13(6).
1966a Rhondda dinosaur: Bartholomai, P. 148, fig. (second).

Age: Blackstone Fm. (at Rhondda colliery, near Ipswich).

Material: Single track (QM F5474)

Remarks: The Rhondda dinosaur tracks are very similar to those of Eubrontes from the Connecticut Valley of North America, but are slightly older (Bartholomai, 1966a)

Plectropterna sp.

1966 perhaps flying reptile: Williams, p. 15.

Age: Blackstone Fm.

REMARKS: These tracks, from the Triassic of Bergin Hill Quarry, Goodna (near Brisbane) are not from a flying reptile, but from *Plectropterna* (Fig. 1). *Plectropterna* has previously been reported only from the Portland Arkose of Connecticut and Massachusetts (Haubold 1971). The single well-preserved track collected (QM F12220) fits the diagnosis (Lull, 1953, p. 250; Haubold, 1971, p. 50) in all but one point: the recurved impression of the hallux. However it is to be noted that Lull states that the hallux is 'usually recurved' (p. 251), and that of the five *Plectropterna* tracks that he illustrates, only two (figs. 124, 126) show the hallux impression as recurved. The Bergin Hill specimen is one of the largest recorded with an overall length of 190 mm.

LOWER JURASSIC

AMPHIBIA
O. TEMNOSPONDYLI
F. BRACHYOPIDAE

Austropelor wadleyi Longman 1941

*1941 *Austropelor wadleyi*, Longman, p. 29–32, pl. 5.
1956 *Australopelor:* v. Huene p. 97.
1960 *Austropelor wadleyi*, d. Jersey in Cameron et al., p. 291.
1964 *Austrapelor:* Konzhukova, p. 63.
1964 *Austrapelor*, Tatarinov p. 57.
1966 *Austropelor wadleyi*, Hill, Playford & Woods, pl. J15(3).

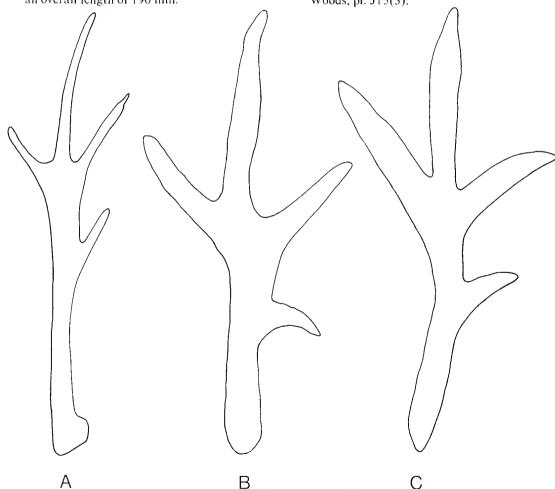A   B   C

FIG. 1. Tracks of *Plectropterna*. A, *P.* sp. (QM F12220) from the Upper Triassic Blackstone Fm., of Goodna, near Brisbane, Queensland; B, *P. minitans* from Massachusetts; and, C. *P. gracilis* also from Massachusetts. A, c. 1/3 x, B, c. 1/2 x, C, c. 1x. (B and C after Lull, 1953.)

1967   *Austropelor wadleyi*, Colbert, p. 35–42, pl. 6.
1969   *Austropelor*, Laseron & Brunnschweiler p. 177.
1970   *Austropelor wadleyi:* Cameron, p. 5.
1977   *Austropelor wadleyi:* Warren, p. 437.
1980c *Austropelor:* Molnar, p. 50.

AGE: Not conclusively settled it derives from the Marburg Ss. usually considered to be Lower Jurassic. Colbert (1967) however has argued that the Marburg may well be Triassic in age. It is here included as Jurassic from convenience not conviction.

MATERIAL: Jaw fragment (QM F2628).

F. UNCERTAIN

The Kolane labyrinthodont

1977   Kolane amphibian: Warren, p. 436–7, fig. 1.
1977   labyrinthodont: Milner p. 402.
1980a brachyopid labyrinthodont: Molnar, p. 131.
1980c Kolane labyrinthodont: Molnar, p. 50.

AGE: Evergreen Fm.

REPTILIA
O. SAUROPTERYGIA
F. UNCERTAIN

The Kolane plesiosaurs

1980   plesiosaurs: Thulborn & Warren, p. 224–5, fig. 1.

AGE: Evergreen Fm.

F. RHOMALEOSAURIDAE

?Leptocleidus sp.

1966c *Leptocleidus:* Bartholomai, p. 437.
1967   plesiosaurian: Playford & Cornelius, p. 84, 91.
1980c *Leptocleidus:* Molnar, P. 54.

AGE: Razorback beds, Lower Jurassic.

MATERIAL: A large number of natural moulds of vertebrae, teeth, and other elements (QM F3983 – QM F4036 inclusive).

REMARKS: The Lower Jurassic date of the Razorback beds, demonstrated by Playford & Cornelius (1967), casts some doubt on the identification of these remains as

Leptocleidus, a genus hitherto known only from the Lower Cretaceous (Persson, 1963). While date is not a good taxonomic character, the incompleteness of the material and existence of similar forms in the Liassic of western Europe (e.g. *Eurycleidus*) suggests that a redetermination of this material is in order. On the other hand it must be admitted that the characteristic deep transverse processes of the anterior dorsals characterising *L. superstes* (Andrew, 1922; Bartholomai, 1966c) are clearly present on the Mount Morgan material. Perhaps freshwater plesiosaurs originated in Australia. My comments on this occurrence (Molnar, 1980c) must now be regarded as invalidated by this 'new' dating.

TRACKS

Theropod tracks

1954   dinosaurs: Colliver, p. 78
1954   dinosaur footprints: Staines, p. 483–5, two figs.
1966a dinosaur footprints: Bartholomai, p. 150.
1967   theropods: Playford and Cornelius, p. 84.
1980   theropod footprints: Molnar, p. 131.

AGE: Lower Jurassic.

REMARKS: My comments on this occurrence (Molnar, 1980a) have been invalidated by the dating of these beds as Lower Jurassic by Playford & Cornelius (1967). These tracks are just what would be expected of Lower Jurassic theropod tracks.

O. SAURISCHIA
F. UNCERTAIN

Rhoetosaurus brownei Longman 1926

1926   a dinosaurus: Jensen, p. 49.
*1926 *Rhoetosaurus brownei:* Longman, p. 183–94, pls. 29–33.
1927   *Rhoetosaurus brownei:* Longman, p. 1–18, figs. 1–4, pls. 1–5.
1929   *Rhoetosaurus brownei:* Longman, p. 249–50, pl. 29. (Reconstruction).
1932   *Rhoetosaurus brownei:* v. Huene, p. 255–6, 312. (Bibliographic entry only on 312).
1950   *Rhaetosaurus brownei:* David, p. 468
1955   *Rhoetosaurus:* d. Lapparent & Lavocat, p. 821.
1956   *Rhoetosaurus:* v. Huene, p. 500.
1964   *Rhoetosaurus brownei:* Rozhdestvenskii, p. 544.

1966　*Rhaetosaurus brownei*: Hill, Playford &
Woods, pl. J15(1). (This is a new illustration,
not reproduced elsewhere).
1969　*Rhaetosaurus*: Lascron & Brunnsch-
weiler, p. 175–6.
1970　*Rhoetosaurus brownei*: Steel, p. 66.
1974　*Rhaetosaurus brownei*: Gould, p. 35.
1981　*Rhoetosaurus brownei*: Coombs &
Molnar, p. 358.

AGE: Probably Injune Creek beds.

MATERIAL: One cervical, dorsals, sacrals and
caudals, ribs, ischia, femur, tibia, fibula, pes
(QM F1695).

REMARKS: The holotype material has also been
given the number QM F1751.

TRACKS

Changpeipus bartholomaii Haubold 1971

1966a dinosaur footprints: Bartholomai, fig.
(third, p. 149).
1966　theropod footprint: Hill, Playford and
Woods, pl. J15(4).
1970　dinosaur footprint, Cameron, p. 9. (In
list only).
*1971　*Changpeipus bartholomaii*: Haubold, p.
79.

AGE: Walloon Gr., at Westvale No. 5 colliery.

MATERIAL: Single track (QM F5700) and cast of
(second) track (QM F12221).

Theropod tracks from the Bruce Seam, Walloon
Gr.

1933　dinosaurian footprints: Ball, p. 384
(Lanefield No. 2 colliery).
1934a dinosaur footprints: Ball, p. 297, three
figs. (Lanefield No. 2).
1934b dinosaurian footprints: Ball, p. 224, three
figs. (Lanefield No. 2).
1946　dinosaur footprints: Ball, p.179, two figs.
(Lanefield No. 2 Extended colliery).
1950　tracks: David, p. 468. (Lanefield).
1952b dinosaur footprints: Anon., p. 950. (Both
collieries).
1958　bipedal form: Hills, p. 99. (Lanefield
No. 2)
1969　dinosaur footprints: Laseron &
Brunnschweiler, p. 175. ("Lanefield
Extended")
1970　dinosaur footprints: Cameron, p. 9.
(Both collieries).

AGE: Walloon Gr.

Theropod tracks from the Wass Seam, Walloon
Gr.

1952b dinosaur footprints: Anon., p. 950.
1970　dinosaur footprints: Cameron, p. 9.

AGE: Walloon Gr.

REMARKS: Cameron (1970) points out that Anon.
(1952b) has incorrectly recorded these tracks
from Lowfield No. 2 colliery when they are in
fact from Westvale No. 6.

Theropod and quadruped tracks

1951　dinosaurs footprints: Anon., p. 583.
1952a dinosaurs footprints: Anon., p. 107, one
fig.
1952b dinosaur footprints: Anon., p. 949–50,
three figs.
1966a theropod dinosaur: Bartholomai, p. 148.
1966　?coelurosaurian footprint: Hill, Playford
& Woods, pl. J15(6).
1966　?stegosaurian footprint: Hill, Playford
& Woods, pl. J15(5).
1969　beast of the *Iguanodon* type: Laseron &
Brunnschweiler, p. 175.
1970　Dinosaur Footprint: Brooks, p. 21, fig.
31.
1974　large theropod footprints: Gould, p.35.

AGE: Walloon Gr.

MATERIAL: Large theropod (QM F3278), small
theropod (QM F5702), ?stegosaur (QM
F5701).

REMARKS: The tracks described by Anon. (1951,
1952a, 1952b) all pertain to large theropods,
as does, probably, that referred to by Laseron
& Brunnschweiler. All references save Gould
(1974) refer to Balgowan colliery, Gould
refers to Roughrigg No. 5 and United No. 8
collieries.

LOWER CRETACEOUS

REPTILIA
O. CHELONIA
F. UNCERTAIN

Cratochelone berneyi Longman 1915

*1915　*Cratochelone berneyi*: Longman, p.
24–9, figs. 1–2, pls. 12–3.
1955　*Cratochelone*: Bergounioux, p. 515.
1960　*Cratochelone berneyi*: Zangerl, p. 309.
1981　*Cratochelone berneyi*: Gaffney, p. 4–5.

AGE: Presumably Toolebuc Fm., Albian.

MATERIAL: Left shoulder girdle, humerus, radius, ulna, plastral fragments (QM F550). Elements all incomplete.

REMARKS: Zangerl (1960) and Gaffney (1981) are both unable to relate this material to known taxa and Gaffney suggests that further material is necessary to determine its relationships.

F. CHELONIIDAE

Notochelone costata (Owen 1882)

*1882b *Notochelys costata:* Owen, p. 178–83, figs. 1–2.
1886 *Notochelys costata:* Etheridge, p. 239–40.
1889a *Notochelone costata:* Lydekker, p. 325.
1889b *Notochelone costata:* Lydekker, p. 70.
1892 *Notochelone costata:* Jack & Etheridge, p. 505.
1911 *Notochelone costata:* d. Vis, p. 3–11, pls. 3–4.
1935 *Notochelone costata:* Longman, p. 239.
1960 *Notochelone costata:* Zangerl, p. 308–9.
1976 *Notochelone:* Gaffney, p. 326.
1981 *Notochelone costata:* Gaffney, p. 5–8, figs. 3–4.

AGE: Toolebuc Fm., Albian.

MATERIAL: Anterior portions of carapace and plastron with some limb material (USDG 6951). Much further material representing almost every portion of the skeleton has been collected by the QM, including at least three almost complete and well preserved skulls.

REMARKS: If all of the small chelonian material of the Toolebuc is referable to this taxon (an assumption needing further study), then it is probably the most abundant tetrapod in the Toolebuc Fm.

Cf. Notochelone

1981 cf. *Notochelone:* Gaffney, p. 7–8.

AGE: Toolebuc Fm., Albian.

MATERIAL: See Gaffney, 1981.

O. SAUROPTERYGIA
F. PLIOSAURIDAE

Kronosaurus queenslandicus Longman 1924

*1924 *Kronosaurus queenslandicus:* Longman, p. 26–8, pl. 4.

1930 *Kronosaurus queenslandicus:* Longman, p. 1–7, figs. 1–4.
1932 *Kronosaurus queenslandicus:* Longman, p. 98, pl. 12. (Restoration).
1935 *Kronosaurus queenslandicus:* Longman, p. 237.
1935 *Kronosaurus queenslandicus:* White, p. 219–28, figs. 1–2, pl. 9.
1940 *Kronosaurus:* White, p. 455.
1950 *Kronosaurus queenslandicus:* David, p. 499.
1955 *Kronosaurus queenslandicus:* d. Saint-Siene, p. 434, fig. 24F.
1956 *Kronosaurus:* v. Huene, p. 409.
1959 *Kronosaurus queenslandicus:* Anon, p. 22–3, three figs. (Includes a photograph of the cervical vertebrae not elsewhere illustrated.)
1959 *Kronosaurus:* Romer & Lewis, p. 1–15, figs. 1–2, one pl.
1962 *Kronosaurus queenslandicus:* Welles, p. 48.
1964 *Kronosaurus queenslandicus:* Novozhilov, p. 331, fig. 331.
1968 *Kronosaurus queenslandicus:* Hill, Playford & Woods, pl.K12(9).
1969 *Kronosaurus:* Laseron & Brunnschweiler, p. 193, pl. 25.

AGE: Not known for type, but referred specimens are from the Wallumbilla Fm., Aptian-Albian.

MATERIAL : Portion of symphyseal region of mandibles (QM F1609).

REMARKS: Welles (1962) has pointed out that the type specimen is so incomplete as to render adequate comparison difficult. More complete material has recently been collected by the QM, which, when reassembled, should prove a more satisfactory neotype.

F. ELASMOSAURIDAE

Woolungasaurus glendowerensis Persson 1960

*1960 *Woolungasaurus glendowerensis:* Persson, p. 11–6, pls. 1–3.
1962 *Woolungasaurus glendowerensis:* Welles, p. 47–8.
1963 *Woolungasaurus:* Persson, p. 22.
1968 *Woolungasaurus glendowerensis:* Hill, Playford & Wood, pl. K12(6–7)

AGE: Wallumbilla Fm., probably Doncaster Mem., Aptian.

MATERIAL: Vertebrae, ribs, scapulae, coracoids, humerus, radius, ulna, ilia, ischia, pubes, femora, meso- or metapodials, phlanges (QM F3567). Elements incomplete.

Woolungasaurus sp.

1960 *Woolungasaurus* sp.: Persson, p. 16–7.
1963 *Woolungasaurus* sp.: Persson, p. 39.
1982 *Woolungasaurus* sp.: Persson, p. 647–55, pls. 1–2.

AGE: Presumably Albian, stratigraphic data not recorded (from near 'Rainscourt', near Richmond).

MATERIAL: Coracoids and two dorsals (QM F2634).

Elasmosaurid, genus et species indet. (*"Plesiosaurus macrospondylus"* M'Coy 1867a).

  *1867a *Plesiosaurus macrospondylus:* M'Coy, p. 356
  1867b *Plesiosaurus macrospondylus:* M'Coy, p. 196
  1868 *Plesiosaurus macrospondylus:* M'Coy, p. 42
  1872 *Plesiosaurus macrospondylus:* Daintree, p. 278 (In list only).
  1892 *Plesiosaurus macrospondylus:* Jack & Etheridge, p. 508, 510.
  1928 *Plesiosaurus macrospondylus:* Howchin, p. 319.
  1960 Elasmosauridae, genus et species indet. I: Persson, p. 18.
  1962 Elasmosauridae, g. et sp. indet.: Welles, p. 49.

MATERIAL: Two associated cervicals (NMV P22548).

F. CIMOLIASAURIDAE?

Cimoliasaurid?, genus et species indet. (*"Plesiosaurus sutherlandi"* M'Coy 1867a)

  *1867a *Plesiosaurus Sutherlandi:* M'Coy, p. 355.
  1867b *Plesiosaurus Sutherlandi:* M'Coy, p. 196.
  1868 *Plesiosaurus Sutherlandi:* M'Coy, p. 42.
  1872 *Plesiosaurus Sutherlandi:* Daintree, p. 278. (In list only).
  1888 *Plesiosaurus Sutherlandi:* Etheridge, p. 167, one pl.
  1892 *Plesiosaurus Sutherlandi:* Jack & Etheridge, p. 508–10.
  1897a *Plesiosaurus sutherlandi:* Etheridge, p. 29.

1904 *Cimoliosaurus sutherlandi:* Etheridge, p. 312.
1960 Cimoliasauridae? genus et species indet. I: Persson, p. 10.
1962 *Plesiosaurus sutherlandi:* Welles, p. 49.

AGE: Uncertain, due to absence of detailed locality data (true also for *"P. macrospondylus"*.)

MATERIAL: One cervical (NMV P22572).

Unidentified or indeterminate plesiosaur material.

1887 *Plesiosaurus:* Etheridge, p. 57. From Pitchery Ck.
1889b *Plesiosaurus:* Etheridge, p. 410–3, pl. 8. From Walsh River (QM F983).
1924 *Elasmosaurus:* Watson, p. 885, 887. From Queensland, no details given.
1935 plesiosaurs: Longman, p. 238–9.
1963 plesiosaurs: Persson, p. 39.

REMARKS: Longman lists material from: near Richmond, 'Caithness' near Dartmouth (QM F2100), 'Baneda' or 'Bareda' near Augathella (QM F2329), 'Ashgrove' near Barcaldine (QM F2299),'Telemon' (QM F2446–F2449), and Mount Abundance near Muckadilla (QM 2176 and QM F2242). Persson lists elasmosaurids (other than *"P. macrospondylus"*) from Richmond (QM F2086), 'Dunluce' near Hughenden (LM L04017), and 'Amby' near Roma (QM F2386); a ?cimoliasaurid from Hughenden (LM L04016); and a polycotylid from 'Wetherby' near Richmond (QM F3307).

O. ICHTHYOSAURIA
F. STENOPTERYGIIDAE

Platypterygius australis (M'Coy 1867a)

  *1867a *Ichthyosaurus australis:* M'Coy, p. 355.
  1867b *Ichthyosaurus australis:* M'Coy, p. 196.
  1868 *Ichthyosaurus australis:* M'Coy, p. 42.
  1869 *Ichthyosaurus australis:* M'Coy, p. 77–8.
  1870 *Ichthyosaurus australis:* M'Coy, p. 228.
  1872 *Ichthyosaurus australis:* Daintree, p. 278. (In list only).
  1889a *Ichthyosaurus australis:* Etheridge, p. 405–9.
  *1889b *Ichthyosaurus marathonensis:* Etheridge, p. 405–9, pl. 7.
  1892 *Ichthyosaurus australis:* Jack & Etheridge, p. 505–6.

1892 *Ichthyosaurus marathonensis:* Jack & Etheridge, p. 505–8.

1897b *Ichthyosaurus australis:* Etheridge, p. 66–8.

1914 *Ichthyosaurus australis:* Chapman, p. 277, fig. 133.

1922 *Myopterygius marathonensis:* v. Huene, p. 98.

1922 *Ichthyosaurus australis:* Longman, p. 246–56, figs. 1–2, pls. 15–6.

1928 *Ichthyosaurus australis:* Howchin, p. 318, fig, 142.

1928 *Ichthyosaurus marathonensis:* Howchin, p. 318.

1928 *Ichthyosaurus:* Wilkins, p. 85, 284.

1935 *Ichthyosaurus australis:* Longman, p. 236.

1943 *Ichthyosaurus australis:* Longman, p. 101–4, one fig., pl. 10.

1950 *"Ichthyosaurus" australis:* David, p. 499.

1968 *Myopterygius australis:* Hill, Playford & Woods, pl. K12(8).

1969 *Ichthyodectes:* Laseron & Brunnschweiler, pl. 24.

1972 *Platypterygius australis:* McGowan, p. 15–7, pls. 3–4. (*I. marathonensis* is synonymized with *P. australis.*)

AGE: Of type uncertain due to lack of detailed locality data, referred specimens derive from the Toolebuc Fm.

MATERIAL: *P. australis:* posterior portion of skull (NMV P12989), vertebrae (NMV P12992), paddle (NMV P12991), rib fragments (NMV P15595, NMV P15596) and sclerotic ring (NMV P12990). *I. marathonensis:* snout (QM F1448).

Unidentified or indeterminate ichthyosaur material

1968 Ichthyosaurian: d Keyser & Lucas, p. 17.

REMARKS: From the Walsh River. Indeterminate and undetermined ichthyosaur material is usually referred to *Platypterygius australis,* on the assumption that this was the only ichthyosaur taxon present.

O. PTEROSAURIA
F. ORNITHOCHEIRIDAE (sensu latu)

aff. *Ornithocheirus* sp.

1980 aff. *Ornithocheirus* sp.: Molnar & Thulborn, p. 361–3, fig. 1.

1980c pteranodontid pterosaur: Molnar, p. 51, fig. 10.

1981 pterosaur: Olshevsky, p. 35. (Reconstruction only.)

AGE: Toolebuc Fm., Albian.

MATERIAL: Symphyscal region of dentary (QM F10613), scapulocoracoid (QM F10612) and incomplete cervical (QM F10614). Other material including an incomplete pelvis and sacrum has recently been collected from the same locality.

O. ORNITHISCHIA
F. UNCERTAIN

Minmi paravertebra Molnar 1980

1980a small ankylosaur: Molnar, p. 132

*1980b *Minmi paravertebra:* Molnar, p. 77–87, figs. 1–2, pl. 1.

1980c *Minmi paravertebra:* Molnar, p. 51, figs. 8–9. (includes a figure not published in 1980b).

1981 *Minmi paravertebra:* Olshevsky, p. 35. (Reconstruction only.)

AGE: Bungil Fm., Minmi Mem., Aptian.

MATERIAL: Dorsals, ribs, paravertebrae, ventral armour, pes (QM F10329). Most elements incomplete.

REMARKS: The statement (Molnar, 1980b, p. 77) that *Minmi* is the only vertebrate from the Minmi Mem. is incorrect. There is also a plesiosaur (QM L32) and a fish scale (Day, 1976, p. 138).

F. IGUANODONTIDAE

Muttaburrasaurus langdoni Bartholomai & Molnar 1981

1966a bipedal herbivorous dinosaur: Bartholomai, p. 150

1968 iguanodontid: Hill, Playford & Woods, pl. K12(10).

1973a perhaps *Iguanodon:* Colbert, p. 407.

1973b *Iguanodon:* Colbert, p. 182, 184.

1980a large ornithopod: Molnar, p. 132.

*1981 *Muttaburrasaurus langdoni:* Bartholomai & Molnar, p. 319–49, figs. 1–13, pls. 1–2.

1981 Muttaburra iguanodontid: Olshevsky, p. 35. (Reconstruction only).

AGE: Mackunda Fm., Albian.

MATERIAL: Most of skeleton lacking tail (QM F6140, also numbered QMV F6095 in error).

REMARKS: My criticism (Molnar, 1980a) of Colbert's comments relating this form to *Iguanodon* (1973a, 1973b) turned out in the light of Dodson's work on *Camptosaurus* (1980) to lack substance. While I now feel that *M. langdoni* is more closely related to *Camptosaurus* than to *Iguanodon*, it is an iguanodontid as Colbert had contended and his biogeographic comments still stand.

Unidentified   or   indeterminate   ornithischian material

1980a large ornithopod: Molnar, p. 132. From Allaru Mudstone, near Hughenden.
1980a ankylosaur: Molnar, p. 132. From Toolebuc Fm., near Boulia.

MATERIAL: Ornithopod: scapula (QM F10942). Ankylosaur: armour, ribs, vertebrae (QM unnumbered, on loan to BMNH).

O. SAURISCHIA
F. UNCERTAIN

Austrosaurus mckillopi Longman 1933

*1933 *Austrosaurus mckillopi:* Longman, p. 131–43, figs. 2–3, pls. 15–7.
1966a *Austrosaurus:* Bartholomai, p. 150.
1969 *Austrosaurus:* Laseron & Brunnschweiler, p. 192.
1970 *Austrosaurus mckillopi:* Steel, p. 81–2.
1980a *Austrosaurus mckillopi:* Molnar, p. 132
1981 *Austrosaurus mckillopi:* Coombs & Molnar, p. 358.

AGE: Allaru Mudstone, Albian.

MATERIAL: Dorsals and ribs (QM F2316), most incomplete.

REMARKS: Much of the material has yet to be fully prepared. The type locality was visited in 1976 in the hope of finding more material, but nothing of significance (other than some ichthyosaur material) could be found.

Unidentified or indeterminate saurischian material

1980a sauropod: Molnar, p. 132.
1980c sauropod: Molnar, p. 54, fig. 12.
1981 very large sauropod: Bartholomai & Molnar, p. 319
1981 Hughenden sauropod: Olshevsky, p. 35 (Reconstruction only).

REMARKS: Two different specimens are involved here, possibly representing one taxon. I (1980a, 1980c) refer to an incomplete humerus (QM L349) from the Albian of 'Silver Hills, near Hughenden. Olshevsky's reconstruction and the reference by Bartholomai & Molnar are based on an incomplete cervical (QM F6142) from Pelican near Hughenden, that very closely resembles the corresponding material of *Brachiosaurus brancai*.

Unidentified or indeterminate reptilian material

1928 saurian: Wilkins, p. 113, 115

REMARKS : These were found at 'Glendower', from which *Woolungasaurus glendowerensis* was later described (Persson, 1960).

UPPER CRETACEOUS

REPTILIA

O. SAURISCHIA
F. UNCERTAIN

Austrosaurus sp.

1966a armoured dinosaur: Bartholomai, p. 150.
1980a sauropod: Molnar, p. 132.
1980b sauropod: Molnar, p. 77
1980c *Austrosaurus* sp.: Molnar, p. 54, figs. 12–3.
1981 *Austrosaurus* sp.: Coombs & Molnar, p. 351–60, pls. 1–6.
1981 *Austrosaurus mckillopi:* Olshevsky, p. 35. (Restoration only).

AGE: Winton Fm., probably Cenomanian.

MATERIAL: Incomplete elements of the fore and hind limbs and girdles and tail, and a single incomplete dorsal centrum (QM F3390, QM F6737, QM F7291, QM F7292 and QM F7880). It is assumed, but not certain, that all specimens pertain to a single taxon.

TRACKS

1979 dinosaur tracks: Knowles, p. 64–5, two figs.
1979 carnosaur, coelurosaur and ornithopod tracks: Thulborn & Wade, p. 275–9, figs. 1–2.
1979a carnosaur, coelurosaur and ornithopod tracks: Wade, p. 16–21, nine figs.

1979b carnosaur, coelurosaur and ornithopod tracks: Wade, p. 286–91, eight figs.

1980c ornithopod and theropod tracks: Molnar, p. 54.

AGE: Winton Fm., probably Cenomanian.

REMARKS: None of the forms represented by tracks in the Winton are known from skeletal material (in addition to *Austrosaurus* sp. some cranial material of what was possibly a small crocodilian is known), and vice versa.

CENOZOIC

All of the Cenozoic reptilian and amphibian material is grouped together both for convenience and because, except for the extinction of the large forms *(Megalania, Meiolania, Pallimnarchus, Quinkana)* they are much like living forms. Most of the material is Pliocene or Pleistocene, although some dates back to what is probably Eocene. Much reptile and some amphibian material is known from the late Cenozoic of South Australia, although unfortunately little of this has so far been studied.

REPTILIA

O. CHELONIA
F. CHELIDAE

Chelodina sp.

1924   *Chelodina insculpta:* Longman, p. 26.
1981   *Chelodina* sp.: Gaffney, p. 12–14, fig. 8.

AGE: Pliocene? see Gaffney, 1981.

MATERIAL: Anterior half of plastron (QM F1510).

Chelodina sp. *("Chelodina insculpta"* d. Vis 1897)

*1897   *Chelodina insculpta:* d. Vis, p. 5–6, pls. 5–6.
1981   *Chelodina:* Gaffney, p. 16–17, fig. 13b.

AGE: Not known due to lack of detailed locality data.

MATERIAL: Sixteen carapace fragments (QM F1107), and six plastral fragments (QM F1109).

Emydura sp.

1981 *Emydura* sp.: Gaffney, p. 11–12, figs. 6–7.

AGE: Chinchilla Sand, Pliocene

MATERIAL: Anterior portion of shell (QM F7035), anterior portion of plastron (QM F7034), symphyseal region of jaw (QM F9038), and dentary (QM F9039).

Chelid

1981   chelidae: Gaffney, p. 12, 14–15, 21–23.

AGE: Pliocene? and Pleistocene.

MATERIAL: Fragments, see Gaffney, 1981.

F. CHELIDAE

Chelid (= *"Chelymys arata"* d. Vis 1897)

*1897   *Chelymys arata:* d. Vis, p. 5, pl. 4.
1907   *Chelymys arata:* d. Vis, p. 6. (See Gaffney & Bartholomai, 1979, p. 1359.).
1981   Chelidae: Gaffney, p. 15–16, fig. 12.

AGE: Plio-Pleistocene.

MATERIAL: Costal fragment (QM F1099B).

Chelid (= *"Chelymys uberrima"* d. Vis, 1897)

*1897   *Chelymys uberrima:* d. Vis, p. 3–4, pls. 1–2.
1929   *Emydura uberrima:* Longman, p. 248
1981   Chelidae: Gaffney, p. 14–15, figs. 10, 13A.

AGE: Plio-Pleistocene

MATERIAL: Carapace fragments (QM F1104), plastral fragments (QM F1105), nuchal, peripherals and costals (QM 9040).

F. MEIOLANIIDAE

Meiolania oweni Woodward 1888

1881   *Megalania prisca:* Owen, p. 1041–8, pls. 37–8.
1882a *Megalania prisca:* Owen, p. 547–55, pls. 64–5.
1887   *Ceratochelys sthenurus:* Huxley, p. 236.
*1888   *Meiolania oweni:* Woodward, p. 89
1889   *Meiolania oweni:* Lydekker, p. 166–7, fig. 39.
1892   *Meiolania oweni:* Jack & Etheridge, p. 647–8.
1964   *Meiolania:* Sukhanov, p. 359, 361, 393.
1969   *Miolania:* Laseron & Brunnschweiler, p. 223–4.
1981   *Meiolania oweni:* Gaffney, p. 19.

AGE: Pleistocene

MATERIAL: Skull (BMNH R391). A tail club and tail ring (BMNH R392) is referred.

REMARKS: The type skull was described by Owen (1881) as part of the varanoid *Megalania*. For the convoluted history of this taxon see Woodward (1888) and Anderson (1925).

Meiolaniids

1981 Meiolaniidae: Gaffney, p. 19.

AGE: Pliocene?

F. TRIONYCHIDAE

Trionychid (= *"Trionyx australiensis"* d. Vis 1894)

*1894 *Trionyx australiensis:* d. Vis, p. 125–7, pl. 1.
1970 *Trionyx australiensis:* Hill, Playford & Woods, pl. CZ7(8).
1979 Trionychidae: Gaffney & Bartholomai, p. 1354–9, pl. 1.
1981 Trionychidae: Gaffney, p. 18–19.

AGE: Plio-Pleistocene.

MATERIAL: Seven carapace fragments (QM F1101).

Trionychids

1869 *Trionyx:* Clarke, p. 384.
1979 Trionychidae: Gaffney & Bartholomai, p. 1356–7, pls. 1–2.
1981 Trionychidae: Gaffney, p. 18–20.

REMARKS: Several sets of specimens are involved here. These are: QM F2324, QM F2326, QM F2566 and QM F9035 from Boat Mountain near Murgon, which may be Miocene (Molnar, 1982); unnumbered fragments from circa 20 miles east of Emerald, mapped as Pleistocene; QM F9036 from the Leichhardt River, presumably near Floraville Crossing, probably Pleistocene; and, QM F9037 from Fairymeadow near Chinchilla, presumably Pliocene. See Gaffney, 1981.

F. UNCERTAIN

"Chelymys antiqua" d. Vis 1897

*1897 *Chelymys antiqua:* d. Vis, p. 4–5. pl. 3.
1981 Testudines indeterminate: Gaffney, p. 15, fig. 11.

AGE: Plio-Pleistocene.

MATERIAL: Four carapace fragments (QM F1106 A–D).

"Pelocomastes ampla" d. Vis 1897

*1897 *Pelocomastes ampla:* d. Vis, p. 6–7, pl. 7–8.
1907 *Pelocomastes ampla:* d. Vis, p. 6.
1981 Testudines indeterminate: Gaffney, p. 17–18 fig. 14.

AGE: Plio-Pleistocene.

MATERIAL: Four carapace fragments (QM F1102), four plastral fragments (QM 1103).

Unidentified or indeterminate chelonian material

1889 *Chelodina longicollis:* Lydekker, p. 168.
1892 *Chelodina longicollis:* Jack & Etheridge, p. 648.
1907 *Chelymys granulata:* d. Vis, p. 3. (Nomen nudum.)
1927 *Chelodina insculpta:* Jones, p. 39.
1929 chelonians: Longman, p. 248–9. (From Brigalow.)
1950 apparently *Chelodina insculpta:* David, p. 563.
1952 turtle: Riek, p. 6–7, pl. 2(1–2).
1960 chelonian: Cribb, in Cribb et al., p. 353. (From the Narrows near Bundaberg.)
1968 aquatic turtles: Tedford, p. 224.
1976 turtle: Cranfield et al., p. 73. (From the Oxley Gr., near Brisbane).
1981 Testudines indeterminate: Gaffney, p. 20–21.

REMARKS: Several specimens are involved, all (but Longman, 1929, Cribb, 1960, and Cranfield et al., 1976) discussed by Gaffney. These are from: the probably Eocene Redbank Plains Series at Redbank Plains near Brisbane; the possibly Miocene Oakdale Ss. at Boat Mountain near Murgon; the Miocene Carl Creek Ls. at 'Riversleigh'; the Corinda Fm. at Runcorn; the Pliocene Allingham Fm. at 'Bluff Downs'; and the Pleistocene at 'Eton Vale' and at Westbrook. Recently tortoise-like material has also been collected at Redbank Plains.

O. SQUAMATA
F. AGAMIDAE

?*Amphibolurus* sp.

1978 ?*Amphibolurus* sp.: Archer, p. 69. (In faunal list only).

AGE: Pleistocene

MATERIAL: QM F8342.

Chlamydosaurus bennettii Owen, in Bennett 1876a

*1876a *Chlamydosaurus bennettii:* Owen, in Bennett, p. 5.

1876b *Chlamydosaurus bennettii:* Bennett, p. 57.

1888 *Chlamydosaurus kingi:* Lydekker, p. 276.

1892 *Chlamydosaurus bennettii:* Jack & Etheridge, p. 648–9. (Note that their citation of the type description is incorrect).

1928 *Chlamydosaurus bennettii:* Howchin, p. 657.

AGE: Pleistocene

MATERIAL: Jaw (BMNH R495).

REMARKS: This material could stand restudy to determine its taxonomic status.

F. SCINCIDAE

Tiliqua sp.

1978b *Tiliqua* sp.: Molnar, p. 157. (In faunal list only.)

AGE: Pleistocene

MATERIAL: Maxilla (QM F10178).

F. VARANIDAE

Megalania prisca Owen 1858

1858 *Megalania prisca:* Owen, p. 273 (Abstract only.)

*1860 *Megalania prisca:* Owen, p. 43–8, pls. 7–8 (the vertebrae only).

1876a *Megalania prisca:* Bennett, p. 8.

1881 *Megalania prisca:* Owen, p. 1037–40, pls. 34–6.

1882a *Megalania prisca:* Owen, p. 547–55, pls. 64–5.

1886a *Notiosaurus dentatus:* d. Vis, p. 25–32, pls. 1–3.

1888 *Megalania (?Varanus) prisca:* Woodward, p. 89.

1889 *Varanus priscus:* Lydekker, p. 284–6, fig. 66.

*1889 *Varanus dirus:* d. Vis, p. 97–8, pl. 4.

1889 *Megalania:* d. Vis, p. 93–7, pl. 4.

1900 *Varanus dirus:* d. Vis, p. 6, pl. 3.

1917 *Megalania prisca:* Etheridge, p. 126–7, pl. 8.

1918 *Megalania prisca:* Fejervary, p. 445–62, figs. 29–37. *(N. dentatus* is synonymized with *M. prisca.)*

1918 *Varanus dirus:* Fejervary, p. 412–6, figs. 15–6.

1924 *Megalania prisca:* Longman, p. 21–2.

1928 *Notiosaurus dentatus:* Howchin, p. 658.

1928 *Varanus dirus:* Howchin, p. 658.

1930 *Varanus (Megalania) priscus:* Anderson, p. 313–6, pl. 51.

1935 *Megalania prisca:* Fejervary, p. 3–6, 10–38, figs. 1–4, pls. 1–3.

1935 *Megalania prisca:* Longman, p. 237–8.

1950 *Megalania prisca:* David, p. 644.

1970 *Megalania prisca:* Hill, Playford & Woods, pl. CZ7(9)

1970 *Varanus dirus:* Hill, Playford & Woods, pl. CZ7(10).

1975 *Megalania prisca:* Hecht, p. 239–49, pls. 17–8. *(V. dirus* is synonymized with *M. prisca.)*

1979 *Megalania:* Rich & Hall, p. 310–3, five figs. (Reconstruction of skeleton).

1981 *Megalania:* Molnar, p. 834.

AGE: Pleistocene.

MATERIAL: Three incomplete dorsals (BMNH 3209a, BMNH 3209b, BMNH 3209c). See Lydekker (1888) for further comment.

REMARKS: Hecht (1975) argued that the maxilla assigned by Fejervary (1918: see also d. Vis, 1900) cannot with certainty be assigned to either *Megalania* or *Varanus* in the absence of certain comparable material of *M. prisca.* Anderson (1930, p. 311–3, pl. 50) does not pertain to *Megalania.*

Megalania sp.

1975 the Pliocene species: Hecht, p. 246.

AGE: Chinchilla Sand, Pliocene.

MATERIAL: Dorsal and caudal vertebrae (QM C20, QM C106).

Varanus emeritus d. Vis 1889

*1889 *Varanus emeritus:* d. Vis, p. 98–9, pl. 4.

1892 *Varanus emeritus:* Jack & Etheridge, p. 651.

1918 *Varanus emeritus:* Fejervary, p. 416–8, fig. 17.

1928 *Varanus emeritus:* Howchin, p. 658.

AGE: Pleistocene

MATERIAL: Distal humerus (QM F875).

REMARKS: This material could stand restudy to determine its taxonomic status.

Varanus sp.

1976   *Varanus* sp.: Archer & Wade, p. 384–5, pl. 54(h).

1978b *Varanus* sp.: Molnar, p. 157. (In faunal list only).

1979   *Varanus* sp.: Tyler, p. 85.

REMARKS: Tyler comments on the two earlier references. Archer and Wade's report is based on two vertebrae (QM F7774, QM F7777) and a crown (QM F7813) from the Pliocene Allingham Fm. at 'Bluff Downs'. Molnar's report is based upon a sacrum (QM F10183) from the Pleistocene cave deposits at Tea Tree Cave near Chillagoe.

F. BOIDAE

?*Morelia* sp.

1976   ?*Morelia* sp.: Archer & Wade, p. 383, 385.

AGE: Allingham Fm., Pliocene.

MATERIAL: "Three vertebrae (including F7775)" (Archer & Wade, 1976, p. 385).

Unidentified or indeterminate squamatan material

1925   ophidian: Longman, p. 111–2. (From Marmor.)

1934   extinct Python: Chapman, p. 55. (Refers to Longman, 1925.)

1950   snake: David, p. 644. (Refers to Longman, 1925)

1976   ?elapid; agamid similar to *Amphibolurus* sp.: Archer & Wade, p. 234–5. (From Allingham Fm.)

1978   frog, unident.; ?lizard, unident.; lizard, indet.; geckonid, indet.; second geckonid, unident.; ?agamid; snake, unident.: Archer, p. 63, 68–71. (From the Texas Caves Pleistocene, although the indet. lizard is younger than the other material.)

1978b a snake: Molnar, p. 157. (From Tea Tree Cave, in faunal list only.)

O. CROCODILOMORPHA
F. CROCODYLIDAE

Crocodylus porosus Schneider 1801

1888 *Crocodilus porosus:* Lydekker, p. 59.

1892 *Crocodilus porosus:* Jack & Etheridge, p. 652.

1914 *Crocodilus porosus:* Chapman, p. 278

*1924 *Crocodilus nathani:* Longman, p. 23–5, pl. 3.

1925   *Pallimnarchus pollens:* Longman, p. 103–8, pls. 25–6.

1928   *Crocodilus porosus:* Howchin, p. 658.

1934   *Crocodilus porosus:* Chapman, p. 58.

1979   *Crocodylus porosus:* Molnar, p. 357–9, pls. 1–3.

1982   *Crocodylus nathani:* Molnar, p. 663–5, figs. 6–7, pl. 2A–D,E&F. *(C. nathani* synonymized with *C. porosus.)*

1982   *Crocodilus porosus:* Molnar, p. 665–6, fig. 8.

REMARKS: See Molnar (1982).

Pallimnarchus pollens d. Vis 1886b

*1886b *Pallimnarchus pollens:* d. Vis, p. 181–9, pls. 10–4.

1892   *Pallimnarchus pollens:* Jack & Etheridge, p. 652–3.

1907   *Pallimnarchus pollens:* d. Vis, p. 6–7.

1914   *Pallymnarchus pollens:* Chapman, p. 278.

1926   *Pallimnarchus pollens:* Longman, p. 158–9, pl. 18.

1928   *Pallimnarchus polleus:* Howchin, p. 658.

1934   *Pallimnarchus pollens:* Chapman, p. 58.

1937   *Pallimnarchus pollens:* Anderson, p. 77–8, pl. 10.

1950   *Pallimnarchus pollens:* David, p. 644.

1970   *Pallimnarchus pollens:* Hill, Playford & Woods, pl. CZ7 (5).

1982   *Pallimnarchus pollens:* Molnar, p. 658–62, figs. 2–5, pls. 1, 2C, D, I, J. (Lectotype designated.)

REMARKS: See Molnar (1982). Longman (1925 p. 103–8) and Hecht (1975, p. 240) do not refer to *Pallimnarchus.* Chapman (1914,1934) cites localities not elsewhere published (and perhaps incorrect) for both *P. pollens* and *C. porosus.*

Quinkana fortirostrum Molnar 1981

1977   probably ziphodont crocodile: Molnar, p. 62–4, fig. 1.

1978a Chillagoe crocodile: Molnar, p. 3–9, fig. 1.

1978b Chillagoe crocodile: Molnar, p. 156–8.

1979   crocodile: Tyler, p. 98.

*1981   *Quinlana fortirostrum:* Molnar, p. 804–11, figs. 1–4.

AGE: Pleistocene.

MATERIAL: Snout (AM F57844).

Quinkana sp.

1977   xiphodont crocodilian: Hecht & Archer, p. 383–5, fig. 1.
1978   sebecosuchian: Archer, p. 70.
1979   xiphodont: Tyler, p. 98.
1981   *Quinkana* sp.: Molnar, p. 809–11, figs. 6–9.

AGE: Pleistocene.

MATERIAL: Incomplete snout (QM F7898).

REMARKS: The misspelling of ziphodont as 'xiphodont' was introduced by a reviewer of Hecht & Archer and not by the authors.

Unidentified or indeterminate ziphodont crocodilian material.

1930   *Varanus (Megalania) priscus:* Anderson, p. 311–3, pl. 50.
1975   *Pallimnarchus pollens:* Hecht, p. 240.
1981   ziphodont: Molnar, p. 811–5, figs. 10–3.

Unidentified or indeterminate crocodilian material.

1872   Cainozoic crocodile: Daintree, p. 274.
1886b   *Pallimnarchus pollens:* d. Vis, p. 187, 189–91, pls. 14 (1)–5.
1927   *Pallimnarchus pollens:* Jones, p. 39.
1929   *Pallimnarchus pollens:* Longman, p. 249.
1943   crocodilian: Hills, p. 99, pl. 9.
1952   provisionally *Pallimnarchus pollens:* Riek, p. 7.
1960   unnamed crocodilian: Cribb, in Cribb et al., p. 353.
1960   crocodilian: Paten, p. 393.
1968   possibly *Crocodylus:* Tedford, p. 224.
1970   *Crocodilus nathani:* Hill, Playford & Woods, pl. CZ7 (7).
1970   *Pallimnarchus pollens:* Hill, Playford & Woods, pl. CZ7 (6).
1976   *Palimnarchus* sp.: Archer & Wade, p. 234.
1976   crocodile: Cranfield et al., p. 73.
1981   ?ziphodont crocodilian: Molnar, p. 813–5, fig. 11–2.
1982   Murgon crocodilian: Molnar, p. 666.

REMARKS: The crocodilian skin impressions of Riek (1952, pl. 1 fig. 4 and pl. 2 fig. 3) are not crocodilian but probably pertain to some fish, possibly a lungfish. Several of these citations refer to pre-Pliocene material: Cranfield, Cribb, Hills, Jones, Molnar (1982), Paten Riek and Tedford.

SUMMARY SPECIES LIST

LOWER TRIASSIC	*Brachyops allos* Howie 1971
	Keratobrachyops australis Warren 1981
	Parotosuchus gunganj Warren 1980
	Parotosuchus rewanensis Warren 1980
	Deltasaurus? sp.
	Rewana quadricuneata Howie 1972
	Kudnu mackinlayi Bartholomai 1979
	Kadimakara australiensis Bartholomai 1979
	Plectropterna sp. (ichnotaxon)
	Kalisuchus rewanensis Thulborn 1979
UPPER TRIASSIC?	*Agrosaurus macgillivrayi* Seeley 1891
LOWER JURASSIC?	*Austropelor wadleyi* Longman 1941
MIDDLE JURASSIC	*Rhoetosaurus brownei* 1926
	Changpeipus bartholomaii Haubold 1971 (ichnotaxon)
LOWER CRETACEOUS	*Cratochelone berneyi* Longman 1915
	Notochelone costata (Owen 1882)
	Kronosaurus queenslandicus Longman 1924
	Woolungasaurus glendowerensis Persson 1960
	Woolungasaurus sp.
	Platypterygius australis (M'Coy 1867)
	aff. *Ornithocheirus* sp.
	Minmi paravertebra Molnar 1980
	Muttaburrasaurus langdoni Bartholomai & Molnar 1981
	Austrosaurus mckillopi Longman 1933
UPPER CRETACEOUS	*Austrosaurus* sp.
PLIOCENE	*Emydura* sp.
	Megalania sp.
	?Morelia sp.
	Crocodylus porosus Schneider 1801
	Pallimnarchus pollens d. Vis 1886
PLIOCENE?	*Chelodina* sp.
PLEISTOCENE?	*Pallimnarchus pollens* d. Vis 1886

PLEISTOCENE   *Meiolania oweni* Woodward 1888
              ?*Amphibolurus* sp.
              Chlamydosaurus bennettii Owen,
                 in Bennett 1876
              Tiliqua sp.
              Megalania prisca Owen 1858
              Varanus emeritus d. Vis 1889
              Varanus sp.
              Crocodylus porosus Schneider
                 1801
              Quinkana fortirostrum Molnar
                 1981
              Quinkana sp.

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LITERATURE CITED

Works indicated by an asterisk do not refer to Queensland material, but have been cited in other connections.

*ANDERSON, C., 1925. Notes on the extinct chelonian *Meiolania*, with a record of a new occurrence. *Rec. Austral. Mus.* 14: 233–42.

1930. *Meiolania platyceps* Owen and *Varanus (Megalania) priscus* (Owen). *Rec. Austral. Mus.* 17: 309–16.

1937. Palaeontological notes. *Rec. Austral. Mus.* 20: 73–8.

*ANDREWS, C.W., 1922. Description of a new plesiosaur from the Weald clay of Berwick (Sussex). *Quart. J. Geol. Soc. London* 78: 285–298.

ARCHER, M., 1978. Quaternary vertebrate faunas from the Texas Caves of southeastern Queensland. *Mem. Qd Mus.* 19: 61–100.

& M. WADE, 1976. Results of the Ray E. Lemley expeditions, part 1. The Allingham Formation and a new Pliocene vertebrate fauna from northern Queensland. *Mem. Qd Mus.* 17: 379–97.

BALL, L.C., 1933. Fossil footprints. *Qd Gov. Mining J.* 34: 384.

1934a. Fossil footprints. *Qd Gov. Mining J.* 35: 297.

1934b. Fossil footprints. Lanefield colliery, Rosewood district. *Qd Gov. Mining J.* 35: 224.

1946. Dinosaur footprints; Lanefield Extended colliery, Rosewood district. *Qd Gov. Mining J.* 47: 179.

BARTHOLOMAI, A. 1966a. Fossil footprints in Queensland. *Austral. Nat. Hist.* 15: 147–50.

1966b. The discovery of plesiosaurian remains in freshwater sediments in Queensland. *Austral. J. Sci.* 28: 437.

1979. New lizard-like reptiles from the early Triassic of Queensland. *Alcheringa* 3: 225–34.

& A. HOWIE, 1970. Vertebrate fauna from the Lower Trias of Australia. *Nature* 225: 1063.

& R.E. MOLNAR, 1981. *Muttaburrasaurus*, a new iguanodontid (Ornithischia: Ornithopoda) dinosaur from the Lower Cretaceous of Queensland. *Mem. Qd. Mus.* 20: 319–49.

BENNETT, G., 1876a. Notes of rambles in search of fossil remains on the Darling Downs. *Trans. Phil. Soc. Qd.* 1876: 3–10. (Note that volumes are not numbered in this series prior to vol. 3, nor are these volumes sequentially paginated.)

1876b. Notes on the *Chlamydosaurus* or frilled lizard of Queensland (*Chlamydosaurus kingii*, Gray), and the discovery of a fossil species on the Darling Downs, Queensland. *Papers Proc. Rept. Roy. Soc. Tasmania* 1875: 56–8.

BERGOUNIOUX, F.M., 1955. Testudinata. In, J. Piveteau, ed. 'Traite de Paleontologie', T. 5. (Paris: Masson et Cie), p. 487–544.

BROOKS, A.E., 1970. 'Australia in the Making'. (Melbourne: Lothian), 90 p.

CAMERON, J.B., 1970. The Rosewood-Walloon coalfield. *Geol. Surv. Qd Publ.* 344: 1–42.

N.J. d. JERSEY, V.G. SWINDON & E.G. WILSON, 1960. The Ipswich basin. *J. Geol. Soc. Austral.* 7: 287–96.

CHAPMAN, F., 1914. 'Australasian Fossils'. (Melbourne: George Robertson), 341 p.

1934. 'The Book of Fossils'. (Sydney: Shakespeare Head Press), 126 p.

CLARKE, W.B., 1869. *Dinornis* an Australian genus. *Geol. Mag.* 6: 383–4.

COLBERT, E.H., 1967. A new interpretation of *Austropelor*, a supposed Jurassic labyrinthodont amphibian from Queensland. *Mem. Qd Mus.* 15: 35–42.

1973a. Continental drift and the distribution of fossil reptiles. *In,* Tarling, D.H., & S.K. Runcorn, eds., 'Implications of Continental Drift to the Earth Sciences', vol. 1. (New York: Academic Press), 622 p.

1973b. 'Wandering Lands and Animals'. (London: Hutchinson), 325 p.

& J.W. KITCHING. 1975. The Triassic reptile *Procolophon* in Antarctica. *Amer. Mus. Nov.*, **2566**: 1–23.

COLLIVER, F.S. 1954. Triassic footprints in Queensland. *Qd Nat.* **15**: 78–9.

COOMBS, W.P., JR., & R.E. MOLNAR. 1981. Sauropoda (Reptilia, Saurischia) from the Cretaceous of Queensland. *Mem. Qd Mus.* **20**: 351–73.

COSGRIFF, J.W., & J.M. ZAWISKIE. 1979. A new species of the Rhytidosteidae from the Lystrosaurus zone and a review of the Rhytidosteidae. *Palaeont. Afr.* **22**: 1–27.

CRANFIELD, L.C., H. SCHWARZBACH & R.W. DAY. 1976. Geology of the Ipswich and Brisbane 1:250 000 sheet areas. *Geol. Surv. Qd Rept.* **95**: 1–176.

CRIBB, H.G.S., N.R. McTAGGART & H.R.E. STAINES. 1960. Sediments east of the Great Divide. *J. Geol. Soc. Austral.* **7**: 345–55.

DAINTREE, R. 1872. Notes on the geology of the colony of Queensland. *Quart. J. Geol. Soc. London* **28**: 271–360.

DAVID, T.E.E. 1950. 'The Geology of the Commonwealth of Australia', vol. 1. (London: Edward Arnold), 747 p.

DAY, R.W. 1976. Aptian and Albian macrofossils from the Mitchell and Roma 1:250 000 sheet areas. *Bur. Miner. Res. Bull.* **166**: 137–50. (Appendix 1 to N.F. Exon, Geology of the Surat Basin in Queensland).

*DODSON, P. 1980. Comparative osteology of the American ornithopods *Camptosaurus* and *Tenontosaurus*. *Mém. Soc. géol. France* **139**: 81–5.

ETHERIDGE, R., JR. 1886. *Notochelys costata* Owen. *Geol. Mag.* **3**: 239–40.

1887. Remains of *Plesiosaurus*. J. Roy. Soc. N.S.W. **21**:57. (Noted in Etheridge's bibliography, *Rec. Austral. Mus.* **15**: 10, but published anonymously.)

1888. The further discovery of plesiosaurian remains in Queensland. *Ann. Rept. Dept. Mines N.S.W.* **1888**: 167. (Appendix 15E).

1889a. On additional evidence of the genus *Ichthyosaurus* in the Mesozoic rocks ('Rolling Downs Formation') of northeastern Australia. *Proc. Linn. Soc. N.S.W.* **3**: 405–9.

1889b. On additional evidence of the occurrence of *Plesiosaurus* in the Mesozoic rocks of Queensland. *Proc. Linn. Soc. N.S.W.* **3**: 410–3.

1897a. An Australian sauropterygian (*Cimoliosaurus* (sic.)), converted into precious opal. *Rec. Austral. Mus.* **2**: 19–29.

1897b. On a precaudal vertebra of *Ichthyosaurus australis*, McCoy. *Rec. Austral. Mus.* **3**: 66–8.

1904. A second sauropterygian converted into opal, from the Upper Cretaceous of White Cliffs, New South Wales. *Rec. Austral. Mus.* **5**: 306–16.

1917. Reptilian notes: *Megalania prisca*, Owen, and *Notiosaurus dentatus* Owen; lacertilian dermal armour; opalized remains from Lightning Ridge. *Proc. Roy. Soc. Vict.* **29**: 127–33.

FEJERVARY, G.J. 1918. Contributions to a monography on fossil Varanidae and on Megalanidae. *Ann. Mus. Nation. Hung.* **16**: 341–467.

1935. Further contributions to a monograph of the Megalanidae and fossil Varanidae — with notes on recent varanians. *Ann. Mus. Nation. Hung., Pars Zool.* **29**: 1–128.

GAFFNEY, E.S. 1976. The history of turtles in Australia. *Abs. 25th Internat. Geol. Congr.* **1**: 325–6. (Abstract only.)

1981. A review of the fossil turtles of Australia. *Amer. Mus. Nov.*, **2720**.

& A. BARTHOLOMAI. 1979. Fossil trionychids of Australia. *J. Paleo.* **53**: 1354–60.

GALTON, P.M., & M.A. CLUVER. 1976. *Anchisaurus capensis* (Broom) and a revision of the Anchisauridae (Reptilia: Saurischia). *Ann. S. Afr. Mus.* **69**: 121–59.

GOULD, R.E. 1974. The fossil flora of the Walloon coal measures: a survey. *Proc. Roy. Soc. Qd* **85**: 33–41.

HAUBOLD, H. 1971. Ichnia Amphibiorum et Reptiliorum fossilium. *In*, O. Kuhn, ed. 'Handbuch der Palaoherpetologie', T. 18. (Stuttgart: Gustav Fischer Verlag), 124 p.

HECHT, M.K. 1975. The morphology and relationships of the largest known terrestrial lizard, *Megalania prisca* Owen, from the Pleistocene of Australia. *Proc. Roy. Soc. Vict.* **87**: 239–50.

& M. ARCHER. 1977. Presence of xiphodont (sic.) crocodilians in the Tertiary and Pleistocene of Australia. *Alcheringa* **1**: 383–5.

HILL, D., G. PLAYFORD & J.T. WOODS. 1965. 'Triassic Fossils of Queensland'. (Brisbane: Queensland Palaeontographical Society), 32 p.

1966. 'Jurassic Fossils of Queensland'. (Brisbane: Qd Palaeontog. Soc.), 32 p.

1968. 'Cretaceous Fossils of Queensland'. (Brisbane: Qd Palaeontog. Soc.), 35 p.

1970. 'Cainozoic Fossils of Queensland'. (Brisbane: Qd Palaeontog. Soc.), 36 p.

HILLS, E.S. 1943. Tertiary fresh–water fishes and crocodilian remains from Gladstone and Duaringa, Queensland. *Mem. Qd Mus.* **12**: 96–100.

1958. A brief review of Australian fossil vertebrates. *In*, T.S. Westoll, ed. 'Studies on Fossil Vertebrates'. (London: University of London, Athlone Press), p. 86–107.

HOWCHIN, W. 1928. 'The Building of Australia and the Succession of Life'. (Adelaide: Government Printer), 750 p.

HOWIE, A. 1971. A brachyopid labyrinthodont from the Lower Trias of Queensland. *Proc. Linn. Soc. N.S.W.* **96**: 268–77.

1972. On a Queensland labyrinthodont. *In*, K.A. Joysey & T.S. Kemp, eds. 'Studies in Vertebrate Evolution'. (Edinburgh: Oliver & Boyd), p. 50–64.

v. HUENE, F. 1906. Ueber die Dinosaurier der Aussereuropaeischen Trias. *Geol. Pal. Abh.* **12**, 2: 99–156.

1922 Die Ichthyosaurier des Lias und ihre Zusammenhänge. *Monog. Geol. Pal.* **1**, 1: 1–114.

1932. Die fossile Reptil–Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monog. Geol. Pal.* **1**, 4: 1–361.

1956. 'Paläontologie und Phylogenie der Niederen Tetrapoden'. (Jena: Gustav Fischer Verlag), 716 p.

HUXLEY, T.H. 1887. Preliminary note on the fossil remains of a chelonian reptile, *Ceratochelys sthenurus*, from Lord Howe's Island, Australia. *Proc. Roy. Soc.* **42**: 232–8.

JACK, R.L., & R. ETHERIDGE, JR. 1892. 'The Geology and Palaeontology of Queensland and New Guinea'. (Brisbane: Government Printer), 768 p.

JENSEN, H.I. 1926. Geological reconnaissance between Roma, Springsure, Tambo and Taroom. *Publ. Geol. Surv. Qd* **277**: 1–215.

JONES, O.A. 1927. The Tertiary deposits of the Moreton district south-eastern Queensland. *Proc. Roy. Soc. Qd.* **38**: 23–46.

D. KEYSER, F., & K.G. LUCAS. 1968. Geology of the Hodgkinson and Laura Basins, north Queensland. *Bur. Miners, Res. Bull.* **84**: 1–254.

KNOWLES, P.C. 1979. Dinosaur tracks. *Geo* **1** (2): 64–5.

KONZHUKOVA, E.D. 1964. Podklass Apsido-
spondyli. Apsidospondilnie. *In*,O.A. Orlov, ed. 'Osnovi Paleontologii: Zemnovodnie, Presmkaooshchiesa i Ptitsi'. (Moscow: Izdatelstvo 'Nauka'), p. 60–4.

D. LAPPARENT, A.F., & R. LAVOCAT. 1955. Dinosauriens. *In*, J. Pivetau, ed. Traité de Paléontologie, T.5. (Paris: Masson et Cie), p. 785–962.

LASERON, C.F., & R.O. BRUNNSCHWEILER. 1969. 'Ancient Australia', second ed. (New York: Taplinger), 253 p.

LONGMAN, H.A. 1915. On a giant turtle from the Queensland Lower Cretaceous. *Mem. Qd Mus.* **3**: 24–9.

1922. An ichthyosaurian skull from Queensland. *Mem. Qd Mus.* **7**: 246–56.

1924. Some Queensland fossil vertebrates. *Mem. Qd Mus.* **8**: 16–28.

1926. A giant dinosaur from Durham Downs, Queensland. *Mem. Qd Mus.* **8**: 183–94.

1927. The giant dinosaur: *Rhoetosaurus brownei. Mem Qd Mus.* **9**: 1–18.

1929. Palaeontological notes. *Mem. Qd Mus.* **9**: 249–50.

1930. *Kronosaurus queenslandicus*, a gigantic Cretaceous pliosaur. *Mem. Qd Mus.* **10**: 1–7.

1932. Restoration of *Kronosaurus queenslandicus. Mem. Qd Mus.* **10**: 98.

1933. A new dinosaur from the Queensland Cretaceous. *Mem. Qd Mus.* **10**: 131–44.

1935. Palaeontological notes. *Mem. Qd Mus.* **10**: 236–9.

1941. A Queensland amphibian. *Mem. Qd Mus.* **12**: 29–32.

1943. Further notes on Australian ichthyosaurs. *Mem. Qd Mus.* **12**: 101–4.

*LULL, R.S. 1953. Triassic life of the Connecticut Valley. *Connecticut State Geol. Nat. Hist. Surv. Bull.* **81**: 1–331.

LYDEKKER, R. 1888. 'Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History). Part 1. Containing the orders Ornithosauria, Crocodilia, Dinosauria, Squamata, Rhynchocephalia and Proterosauria'. (London: British Museum (Natural History)), 309 p.

1889a. Note on some points in the nomenclature of fossil reptiles and amphibians, with preliminary notice of two new species. *Geol. Mag.* **6**: 325–6.

1889b. 'Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History). Part 3. Containing the order Chelonia'. (London: British Museum (Natural History)), 239 p.

MALONE, E.J., F. OLGERS & A.G. KIRKEGAARD. 1969. The geology of the Duaringa and Saint Lawrence 1:250,000 sheet areas, Queensland. *Bur. Miner. Res. Rept.* **121**: 1–133.

M'COY, F. 1867a. On the occurrence of *Ichthyosaurus* and *Plesiosaurus* in Australia. *Ann. Mag. Nat. Hist.* (3), **19**: 355–6.

1867b. On the Recent zoology and palaeontology of Victoria. *Ann. Mag. Nat. Hist.* (3), **20**: 175–202.

1868. On the discovery of Enaliosauria and other Cretaceous fossils in Australia. *Trans. Proc. Roy. Soc. Vict.* **8**: 41–2.

1869. On the fossil eye and teeth of the *Ichthyosaurus australis* (M'Coy) from the Cretaceous formations of the source of the Flinder's River; and on the palate of the *Diprotodon* from the Tertiary limestone of Limeburner's Pint, near Geelong. *Trans. Proc. Roy. Soc. Vict.* **9**: 77–8.

McGOWAN, C. 1972. The systematics of Cretaceous ichthyosaurs with particular reference to the material from North America. *Contrib. Geol. Univ. Wyoming* **11**: 9–29.

MILNER, A. 1977. Triassic extinction or Jurassic vacuum? *Nature* **265**: 402.

MOLNAR, R.E., 1977. Crocodile with laterally compressed snouth: first find in Australia. *Science* **197**: 62–4.

1978a. The crocodile from Tea Tree Cave and ziphodont crocodiles in Australia. *J. Sydney Speleo. Soc.* **22**: 3–10.

1978b. Age of the Chillagoe crocodile. *Search* **9**: 156–8.

1979. *Crocodylus porosus* from the Pliocene Allingham Formation of north Queensland. Results of the Ray E. Lemley expeditions, part 5. *Mem. Qd Mus.* **19**: 357–65.

1980a. Australian late Mesozoic terrestrial tetrapods: some implications. *Mem. Soc. geol. France.* **139**: 131–43.

1980b. An ankylosaur (Ornithischia: Reptilia) from the Lower Cretaceous of southern Queensland. *Mem. Qd Mus.* **20**: 77–87.

1980c. Reflections on the Mesozoic of Australia. *Mes. Vert. Life* **1**: 47–60.

1981. Pleistocene ziphodont crocodilians of Queensland. *Rec. Austral. Mus.* **33**: 803–34.

1982. *Pallimnarchus* and other Cenozoic crocodiles in Queensland. *Mem. Qd Mus.* **20**: 657–73.

& R.A. THULBORN. 1980. First pterosaur from Australia. *Nature* **288**: 361–3.

MOORE, C. 1870. Australian Mesozoic geology and palaeontology. *Quart. J. Geol. Soc. London* **26**: 226–61.

NOVOZHILOV, N. 1964. Nadsemeistvo Pliosauroidea. *In,* O.A. Orlov, ed. 'Osnovi Paleontologii: Zemnovodnie, Presmkaooshchiesia i Ptitsi'. (Moscow: Izdatelstvo 'Nauka'), p. 327–32.

OLSHEVSKY, G. 1981. Dinosaur renaissance. *Sci. Digest* **87**, 7: 34–43. (Contains restorations of Australian dinosaurs, but no textual material).

OWEN, R. 1858. Description of some remains of the gigantic land-lizard (*Megalania prisca,* Owen), from Australia. *Proc. Roy. Soc.* **9**: 273. (Abstract only).

1860. Description of some remains of the gigantic land-lizard (*Megalania prisca,* Owen), from Australia. *Phil. Trans. Roy. Soc.* **149**: 43–8.

1881. Description of some remains of the gigantic land-lizard (*Megalania prisca,* Owen), from Australia. Part II. *Phil. Trans. Roy. Soc.* **171**: 1037–49.

1882a. Description of some remains of the gigantic land-lizard (*Megalania prisca,* Owen), from Australia. Part III. *Phil. Trans. Roy. Soc.* **172**: 547–55.

1882b. On an extinct chelonian reptile (*Notochelys costata,* Owen), from Australia. *Quart. J. Geol. Soc. London* **38**: 178–83.

PATEN, R.J. 1960. Lacustrine sandstones and limestones and spring sinters of far western Queensland. *J. Geol. Soc. Austral.* **7**: 391–3.

PERSSON, P.O. 1960. Lower Cretaceous plesiosaurians (Rept.) from Australia. *Lunds Univ. Arsskr.,* avd. 2, **56,** 12:1–23.

1963. A revision of the classification of the Plesiosauria with a synopsis of the stratigraphical and geographical distribution of the group. *Lunds Univ. Arsskr.,* avd. 2, **59,** 1: 1–60.

1982. Elasmosaurid skull from the lower cretaceous of Queensland (Reptilia: Sauropterygia), *Mem. Qd. Mus.* **20**: 647–55.

PLAYFORD, G., & K.D. CORNELIUS. 1967. Palynological and lithostratigraphic features of the Razorback beds, Mount Morgan district, Queensland. *Dept. Geol. Univ. Qd Papers* **6**: 81-94.

RICH, T.H. & B. HALL. 1979. Rebuilding a giant. *Austral. Nat. Hist.* **19**: 310–3.

RIEK, E.F. 1952. The fossil insects of the Tertiary Redbank Plains Series. Part 1: An outline of the fossil assemblage with descriptions of the fossil insects of the orders Meeoptera and Neuroptera. *Univ. Qd Papers Dept. Geol.* **4**: 3–14.

ROMER, A.S., & A.D. LEWIS. 1959. A mounted skeleton of the giant plesiosaur *Kronosaurus.* *Breviora* **112**: 1–15.

ROZHDESTVENSKII, A.K. 1964. Podotriad Sauropoda. Zauropod. In, O.A. Orlov, ed. 'Osnovi Paleontologii: Zemnovodnie, Presmkaooshchiesia i Ptitsi'. (Moscow: Izdatelstvo 'Nauka'), p. 543–52.

D. SAINT-SEINE, P. 1955. Sauropterygia. *In,* J. Piveteau, ed. 'Traite de Paleontologie', T. 5. (Paris: Masson et Cie), p. 420–58.

SEELEY, H.G. 1891. On *Agrosaurus macgillivrayi,* a saurischian reptile from the NE–coast of Australia. *Quart. J. Geol. Soc. London* **47**: 164–5.

STAINES, H.R.E., 1954. Dinosaur footprints at Mount Morgan. *Qd Gov. Mining. J.* **632**: 483–5.

   & J.T. WOODS. 1964. Recent discovery of Triassic dinosaur footprints in Queensland. *Austral. J. Sci.* **27**: 55.

STEEL, R. 1970. Saurischia. In, O. Kuhn, ed. 'Handbueh der Palaoherpetologie', T. 14. (Stuttgart: Gustav Fischer Verlag), 87 p.

STEVENS, N.C. 1973. 'A Guidebook to Field Geology in Southeast Queensland'. (Brisbane: University of Queensland Press), 131 p.

SUKHANOV, V.B., 1964. Podklass Testudinata. Testudinati. In, O.A. Orlov, ed. 'Osnovi Paleontologii: Zemnovodnie, Presmkaooshehiesia i Ptitsi'. (Moscow: Izdatelstvo 'Nauka'), P. 354–438.

TATARINOV, L.P. 1964. Obshchaia chast. In, O.A. Orlov, ed. 'Osnovi Paleontoogii: Zemnovodnie, Presmkaooshehiesia i Ptitsi'. (Moscow: Izdatelstvo 'Nauka'), p. 25–59.

THULBORN, R.A. 1979. A proterosuehian thecodont from the Rewan Formation of Queensland. *Mem. Qd Mus.* **19**: 331–55.

   1980. The ankle joint of arehosaurs. *Alcheringa* **4**: 241–61.

   & M. WADE. 1979. Dinosaur stampede in the Cretaeeous of Queensland. *Lethaia* **12**: 275–9.

   & A. WARREN. 1980. Early Jurassie plesiosaurs from Australia. *Nature* **285**: 224–5.

TYLER, M.J. 1979. Herpetofaunal relationships of South America with Australia. *Monog. Mus. Nat. Hist. Univ. Kansas* **7**: 73–106.

De VIS, C.W. 1886a. On bones and teeth of a large extinet lizard. *Proc. Roy. Soc. Qd* **2**: 25–32.

   1886b On remains of an extinet saurian. *Proc. Roy. Soc. Qd* **2**: 181–91.

   1889. On *Megalania* and its allies. *Proc. Roy. Soc. Qd* **6**: 93–9.

   1894 The lesser ehelonians of the nototherian drifts. *Proc. Roy. Soc. Qd* **10**: 123–7.

   1897. The extinct fresh-water turtles of Queensland. *Ann. Qd Mus.* **3**: 3–7.

   1900. A further traee of an extinet lizard. *Ann. Qd Mus.* **5**:6. (This paper bears no indication of author, however on the title page of this volume is stated 'Annals of the Queensland Museum. No. 5. By C.W. de Vis, M.A. Direetor'. This, together with the absence of other fossil vertebrate workers in Queensland at this time, suggests to me, as it did to Fejervary (1918) that de Vis wrote this paper.).

   1907. Fossils from the Gulf watershed. *Ann. Qd Mus.* **7**: 1–7.

   1911. On some Mesozoic fossils. *Ann. Qd Mus.* **10**: 1–11.

WADE, M. 1979a. A minute — a hundred million years ago. *Hemisphere* **23**: 16–21.

   1979b. Tracking dinosaurs: the Winton excavation. *Austral. Nat. Hist.* **19**: 286–91.

WARREN, A. 1972a. Queensland trace fossils pose a 230 million year old problem. *Austral. Nat. Hist.* **17**: 279–83.

   1972b. Triassic amphibians and reptiles of Australia in relation to Gondwanaland. *Austral. Nat. Hist.* **17**: 279–83.

   1977. Jurassic labrynthodont. *Nature* **265**: 436–7.

   1980. *Parotosuchus* from the early Triassic of Queensland and Western Australia. *Alcheringa* **4**: 25–36.

   1981a. A horned member of the labyrinthodont superfamily Brachyopoidea from the early Triassic of Queensland. *Alcheringa* **5**: 273–88.

   1981b. The lower jaw of the labyrinthodont family Braehyopidae. *Mem. Qd Mus.* **20**: 285–9.

WATSON, D.M.S. 1924. The elasmosaurid shoulder-girdle and fore-limb. *Proc. Zool. Soc. London* **1924**: 885–917.

WELLES, S.P. 1962. A new species of elasmosaur from the Aptian of Colombia and a review of the Cretaceous plesiosaurs. *Univ. Calif. Publ. Geol. Sci.* **44**: 1–96.

WHITE, T.E. 1935. On the skull of *Kronosaurus queenslandicus* Longman, *Occas. Papers Boston Soc. Nat. Hist.* **8**: 219–28.

1940. Holotype of *Plesiosaurus longirostris* Blake and classification of the plesiosaurs. *J. Paleo.* **14**: 451–67.

WILKINS, G.H. 1928. 'Undiscovered Australia'. (London: Ernest Benn), 292 p.

WILLIAMS, K.A.W. 1966. Reptiles. *Qd Nat.* **18**: 9–15.

WOODWARD, A.S. 1888. Note on the extinct reptilian genera *Megalania*, Owen, and *Meiolania*, Owen. *Ann. Mag. Nat. Hist.* (6) **1**: 85–9.

ZANGERL, R. 1960. The vertebrate fauna of the Selma Formation of Alabama. Part V. An advanced cheloniid sea turtle. *Fieldiana: Geol. Mem.* **3**: 279–312.

ANONYMOUS. 1951. Giant dinosaur's footprints found in Darling Downs colliery. *Qd Gov. Mining J.* **52**: 583.

1952a. Dinosaur's footprints in Downs colliery. *Qd Gov. Mining J.* **53**: 107.

1952b. Dinosaur footprints. *Qd Gov. Mining J.* **53**: 949–50.

1959. Ancient monarch of the seas. *Nat. Hist.* **68**: 22–3.

1965. Dinosaur footprints on the ceiling: Queensland, Australia. *Sci. Digest* **57**: ife.

LITORIA REVELATA: A NEW SPECIES OF TREE-FROG
FROM EASTERN AUSTRALIA

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ABSTRACT

Litoria revelata sp. nov. is a member of the *L. ewengii* complex. It is most similar to *L. jervisiensis* but *L. revelata* can be distinguished readily by black spotting in the groin and by the breeding call which has a dominant frequency of around 4kHz.

INTRODUCTION

The existence of the tree-frog described in this paper has been known for nearly twenty years. Straughan (1966) in his unpublished thesis noted its undescribed status, its membership of the *L. ewengii* complex, and its reproductive isolation from *Litoria verreauxii*. The description of this new species was delayed for two reasons. Firstly, the nomenclature and status of closely related species in mid-eastern New South Wales had not been resolved. This has been rectified recently (White, Whitford, and Watson 1980). Secondly, the status of *L. ewengii*-like specimens from northeastern and mid-eastern Queensland (Moore 1961) also had to be resolved. Recently, we located the northern populations of this frog and recorded their choruses.

Measurements are in millimetres and ratios are expressed as percentages. Specimens housed in the Queensland Museum, Australian Museum, National Museum of Victoria, and British Museum of Natural History are prefixed by J, R, D, and BMNH respectively. Abbreviations follow Liem and Ingram (1977).

LITORIA REVELATA sp. nov.

HOLOTYPE: J28233; ♂, O'Reillys (28° 14'S, 153° 08'E), Lamington Plateau, SE. Queensland collected by G.J. Ingram on 6 August, 1973.
PARATYPES: NE. Queensland: Millaa Millaa Lookout (J30116); Millaa Millaa Falls (J30120–1); Lamin's Hill, west side of Mt Bartle Frere (J30137); Sluice Creek Road (J30117–9, 30122–35, 30138–59, D55546, 55568, R99993); Ravenshoe (J13156).
ME. Queensland: Thurgood's Farm 18 km. N. of Dalrymple Heights (J35087, 35105–6, 35115–6); Port Denison (BMNH 64.7.8.11–12).
SE. Queensland: Mt Tamborine (J12853, 19869, 19872, 19910); Lost World (J10896); Springbrook (J19867–8, 19887, 19889–90, 19892–4, 19898, 19909); O'Reillys (J19873, 19900, 19911–2, 19915, 19918, 28233, R99994, D55547); Wilson's Peak (J28232); Lever's Plateau (J31971).
NE. New South Wales: Ballina (J31465, 31467–8, 35543); Tooloom Range (J35539).
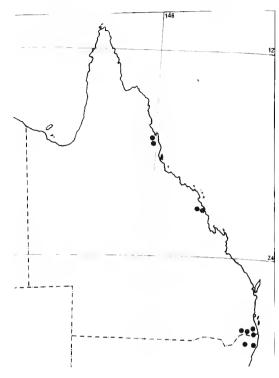
DIAGNOSIS: A member of the *L. ewingii* group (*sensu* Tyler and Davies, 1978) but distinguished from other members by a combination of prominent terminal discs much wider than the digits, and the presence of black spots in the inguinal regions. The breeding call is also diagnostic in having the dominant frequency around 4kHz.

DISTRIBUTION: Northeastern Queensland to northeastern New South Wales (Fig. 1). There are three disjunct populations. These are on the Atherton Tableland and Bellenden-Ker Range, NE.Qd, Eungella Plateau, ME.Qd, and the extreme corner of SE.Qd–NE.NSW on the Great

FIG. 1. Distribution of *Litoria revelata*.

Divide, Macpherson Range, Tamborine Mountain, Tooloom Range and coastal swamps around Ballina. In addition to specimen records, there are two recordings of choruses from inside the Crater, Crater National Park (G. Czechura and G. Ingram, pers.comm.).

DESCRIPTION: SVL 16–36 (N = 79, mean 27·1). HW/SVL 30–37 (N = 75, mean 32·2). TL/SVL 46–59 (N = 75 mean 53). SE/SVL 27–38 (N = 75, mean 32). IN 9–19 (N = 71, mean 13·8). EN 9–20 (N = 72, mean 14·7). IN/EN 75–121 (N = 71, mean 96·7). TW 5–13 (N = 73, mean 9·6). ED/TW 158–280 (N = 73, mean 203).

Dorsal aspect of snout blunt, rounded in profile. Loreal region sloping. Canthus rostralis distinct and concave. Pupil horizontal and oval shaped. Supratympanic fold present. Tympanum exposed. Tongue oval, hinged in front. Vomerine teeth in two separate rows in line with posterior edge of choanae.

Fingers webbed basally, distal segments expanded into discs; discs much wider than ends of digits. Length of fingers from shortest to longest 1–2–4–3. Subarticular tubercles present, single. Palmar tubercles usually present, variable in number.

Hindlimbs long. Distal segments of toes expanded into discs; discs much wider than ends of digits. Length of toes from shortest to longest 1–2–3–5–4. Subarticular tubercles present. Toes moderately webbed; webbing formula (see Schiøtz 1967) I–1, IIi–1, IIo–½, IIIi–2, IIIo–1, IVi–½.

Dorsal surface smooth except for a transverse row of raised tubercles (usually 4) between eyes; colour varies from creamy brown to reddish brown; a dark lyre-shaped pattern (typical of the *L. ewingii* complex) can be present. Ventrally cream, usually with brown flecking.

Laterally, a thick dark line begins at tip of snout and continues back to eye, recommences behind eye, continues through and encompasses the tympanum and terminates above arm; an upper labial streak begins at snout, becomes thicker under eye and continues back to subaural gland. Groin usually with 1–3 black spots. Posterior surface of thighs cream (orange in life) lined with varying amounts of black.

CALL: To the ear, the male breeding call of *L. revelata* sounds like a series of high pitched whirrings.

A sound spectrograph of this call is given in Figure 2. This is based on recordings by Chris Corben at O'Reillys, Lamington Plateau, SE. Queensland on 5 October, 1977. Dominant frequency is around 4·1 kHz, note duration is approximately 0·18 seconds and note repetition rate is about 4 Hz. Each note consists of between 15 and 18 pulses (mean 16·4) at a pulse repetition rate of about 87 Hz. Call duration is 2 to 10 seconds consisting of 8 to 40 notes. A breeding call from the Atherton Tableland is similar in structure but is slightly higher pitched (average dominant frequency 4·3 kHz) and the pulse rate is about 1·4 times faster. The average number of pulses per note is 17·1 (range 16–19). These values fall within the range of data for SE. Queensland (Straughan 1966). Calls from the Eungella Plateau sound similar to both those from NE. Queensland and SE. Queensland–NE. New South Wales.

REMARKS

L. revelata breeds in still ponds and swamps. The males call from reeds and grasses around or in the water. Amplexus is axillary. In the mountains of SE Queensland–NE New South Wales it overlaps and even breeds in the same ponds as *L. verreauxii*. In Queensland *L. revelata* is a montane frog but in New South Wales it also occurs around coastal swamps and ponds near
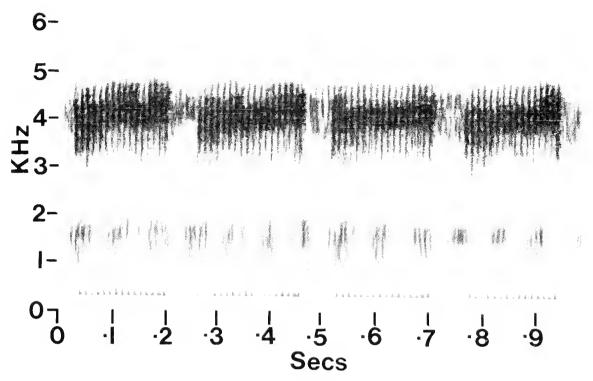
FIG. 2. Sonograph of the call of *Litoria revelata*.

Ballina. *L. jervisiensis* also has been recorded from the Ballina area (White et al 1980) and it is possible that the two may be found to overlap. Although *L. revelata* more closely resembles *L. jervisiensis* than other species of the *L. ewingii* group, the great differences in breeding call can be expected to act as an effective premating isolating mechanism.

ACKNOWLEDGEMENTS

We thank Greg Czechura for his assistance in the preparation of the paper. Arthur White provided useful advice. Mr. A. Stimson, British Museum of Natural History, kindly allowed us access to specimens in his care.

LITERATURE CITED

LIEM, D.S. and G.J. INGRAM, 1977. Two new species of frogs (Anura: Myobatrachidae, Pelodryadidae) from Queensland and New South Wales. *Vict. Nat.* **94**: 255–62.
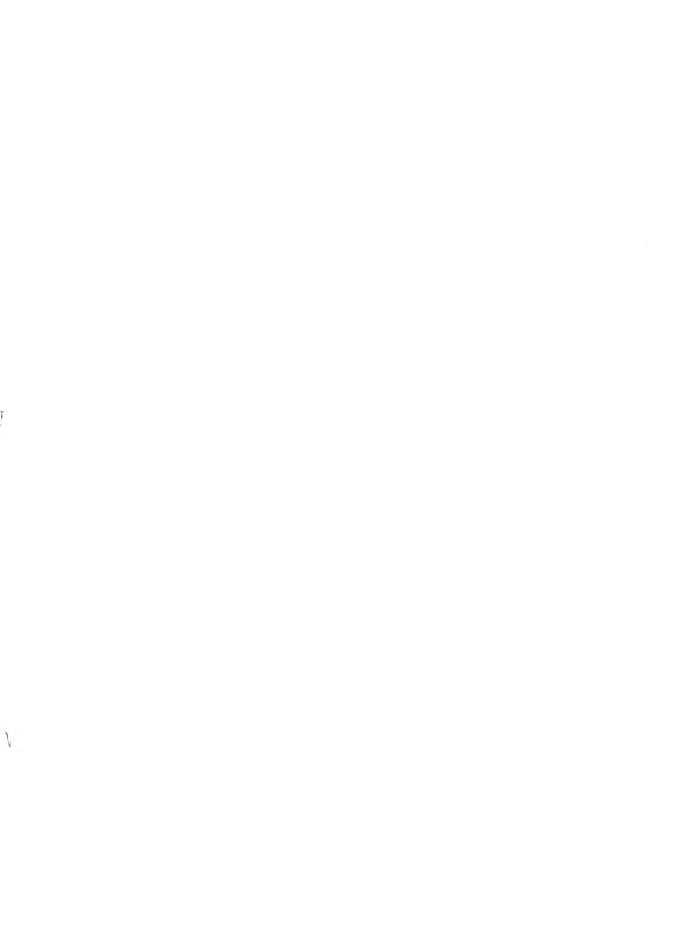
MOORE, J.A. 1961. The frogs of eastern New South Wales. *Bull. Amer. Mus. Nat. Hist.* **121**: 149–386.

SCHIØTZ, A. 1967. The tree frogs (Rhacophoridae) of West Africa. *Spolia Zool. Mus. haun.* **25**: 1–346.

STRAUGHAN, I.R. 1966. 'An analysis of the mechanism of sex and species recognition and species isolation in certain Queensland frogs'. (Unpublished Ph.D. thesis: University of Queensland).

TYLER, M.J. and M. DAVIES, 1978. Species–groups within the Australopapuan hylid frog genus *Litoria* Tschudi. *Aust. J. Zool. Supp..Ser.* **63**: 1–47.

WHITE, A.W., D. WHITFORD, and G.F. WATSON, 1980. Re-description of the Jervis Bay Tree Frog *Litoria jervisiensis* (Anura: Hylidae), with notes on the identity of Krefft's Frog *(Litoria krefftii). Aust. Zool.* **20**(3): 375–90.

THREE NEW STRIPED SKINKS, (*CTENOTUS*, LACERTILIA, SCINIDAE) FROM QUEENSLAND.

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ABSTRACT

Ctenotus arcanus sp. nov., *Ctenotus eurydice* sp. nov., and *Ctenotus ingrami* sp. nov. are described from eastern Queensland and adjacent northern New South Wales. A key to the *Ctenotus* species of southeastern Queensland is provided.

INTRODUCTION

Ingram and Covacevich (1981) recognize a total of twenty-three species of *Ctenotus* occurring in Queensland. In addition the following species may be added to this list, *C. piankai* Storr, *C. eutaenius* Storr, *C. monticola* Storr, *C. capricorni* Storr, *C. zebrilla* Storr and *C. allotropis* Storr (Storr 1970, 1981).

Recent investigations of Queensland populations of *Ctenotus taeniolatus* (Shaw) indicate that this species is composite and includes three forms readily distinguishable by colouration and size (max. SVL : 76–87 mm) from sympatric *C. taeniolatus*. These three species are the subject of the following paper.

Abbreviations used in the text are as follows: SVL — snout to vent length; TL — tail length; HW — head width; FL — forelimb length; HL — hindlimb length; MBS — midbody scale rows; VS — ventral scales between chin and cloaca; AM — Australian Museum, Sydney; ANWC — Australian National Wildlife Collection, Canberra; QM — Queensland Museum, Brisbane; WAM — Western Australian Museum, Perth. All measurements are recorded in millimetres. Terminology follows Smith (1946). Descriptions are based on hypodigm (e.g. Storr 1970, 1975). The species groups of Storr (1981) are recognized here.

Ctenotus arcanus sp. nov.
Fig. 1. Pl, 1-1.

HOLOTYPE. QM J36925 Coonoon Gibber Creek, Conondale Range southeastern Queensland. Collected during September – October 1978 by D. Milton.

PARATYPES. J11030 10 miles W. of Bundaberg; J30266 Fraser Island; J31863 Glastonbury via Gympie; J38695 Mt Tewantin via Noosa; J30723 Jimna; J34588 Peach Trees via Jimna; J30722 Crohamhurst via Maleny; J12111–2 Cedar Creek Falls, Mt Tamborine; J437–8, J440–2 'south Queensland'; J1682 'Queensland'.

DIAGNOSIS. A moderately large member of the *C. lesueurii* group with 7 (rarely 8) upper labials; 3 or 4 pairs of nuchals; snout rounded in profile; light-edged black mid-dorsal stripe disappearing with age; broad black upper lateral zone with widely spaced, single, white spots; one broad mid-lateral stripe, one narrow dorsolateral stripe along body; ground colour of adult dorsum brown; complex light and dark pattern in parietal region absent; 20–23 callose lamellae under fourth toe; 26–28 mid-body scale rows.

DISTRIBUTION. Coastal southeastern Queensland, Fraser Island and Bundaberg in the north to Mt Tamborine in the south, extending inland only as far as the coastal ranges (Fig. 1).

DESCRIPTION. SVL 66·0 – 87·0 (N = 16, mean 73·6). Length of appendages (%SVL) : TL 182 – 204 (N = 10, mean 189·9) : FL 21·6 – 28·7 (N = 16, mean 24·8) : HL 36·7 – 49·5 (N = 16, mean 44·6).
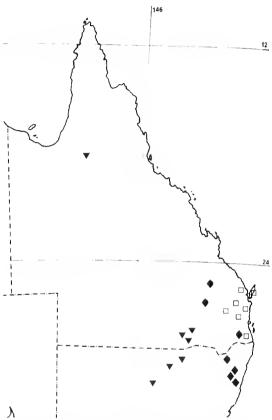
FIG. 1 Distribution of *Ctenotus* species. *C. arcanus* (open squares), *C. eurydice* (closed diamonds) and *C. ingrami* (closed triangles).

Snout rounded in profile. Nasals separated (occasionally in short contact). Prefrontals moderately large, separated. Preoculars 2. Postoculars 1. Supraoculars 4, first three in contact with frontal. Supraciliaries 8–10 (mean, 8·7). Second loreal approximately 1·4 times width of first loreal. Presuboculars 2 (except for holotype where four are present on right side and three on left). Postsuboculars 4–6, usually 5 (mean 5·6). Upper labials 7 (rarely 8), fifth below eye, last three largest. Temporals 1 + 2, upper secondary largest. Ear lobules 3–5 (mean 4·0). Nuchals in 3–5 pairs. MBS 26–28 (mean 27·3). VS 70–81 (mean 75·8). Lamellae under fourth toe 20–23 (mean 21·2), callose with slight lateral compression in some specimens.

Dorsally olive brown. Moderately wide, light-edged, black mid-dorsal stripe in juveniles becoming reduced or absent in adult specimens. In some older specimens the mid-dorsal stripe may remain as a narrow ill-defined black line, more distinct anteriorly. Fine whitish dorsolateral line and broad whitish midlateral line, below which wavy grey markings present. Upper lateral surface black with single series of well spaced white spots, which are less distinct posteriorly and become poorly defined in larger specimens. The white dorsolateral line may be bordered dorsally by a narrow black band.

ETYMOLOGY. The name is taken from the latin *arcanus*, meaning hidden. This refers to the long confusion of this taxon with *C. robustus* Storr and *C. 'taeniolatus'*.

HABITAT. This species occurs in *Eucalyptus* dominated open forest and woodland in coastal areas or adjacent upland areas (Conondale Range, Jimna, Mt Tamborine) or rocky outcrops (Mt Tewantin).

Ctenotus eurydice sp. nov.
Fig. 1. Pl. 1–2.

HOLOTYPE. AM R98372 (formerly QM J34112) Boonoo Boonoo Falls via Tenterfield northeastern New South Wales Collected on 15 December 1978 by G.V. Czechura.

PARATYPES. (Queensland) QM J15614 Coominglah State Forest via Monto; J27526 Marlaybrook, Bunya Mountains via Kingaroy; J39223 Mt Gravatt; J1618 'Queensland'; (New South Wales) AM R59266 3 mi from Nymboidea towards Hortons Ck; R52719 0·5 mi south University of New England, Armidale; R91150 10 mi E. Aspley Falls on Walcha Pt Macquarie Rd.

DIAGNOSIS. A moderately large member of the *C. lesueurii* group; upper labials 7 or 8, nuchals in 4 or 5 pairs; snout rounded in profile with adult pattern consisting of 10 longitudinal pale lines (including wide olive dorsal lines) along body; mid-lateral line entering ear at or near mid-line, not continuous anteriorly; complex light and dark pattern in the parietal — frontal region) 12–23 lamellae under fourth toe; 25–27 midbody scale rows.

DISTRIBUTION. Great Dividing Range in west, as far east as the Brisbane area (Mt. Gravatt). North to Monto and south to the Armidale region of northern New South Wales (Fig. 1).

DESCRIPTION. SVL 56·3–76·6 (N=8, mean 74·3). Length of appendages (% SVL): TL 119·2–229·0 (N=5, mean 179·1): FL 18·3–21·6 (N=8, mean = 20·1): HL 39·2–41·9 (N=8, mean=40·5). Snout rounded in profile. Nasals separated or in short contact. Nostril located anteriorly in nasal. Prefrontals moderately large, separated. Supraoculars 4, first three in contact with frontal. Supraciliaries 8–9 (mean 8·2) first largest. Preoculars 2. Postoculars 1. Second loreal about 1·4 times as wide as first loreal. Presuboculars 2. Postsuboculars 4–6 (mean 5·1). Upper labials 7 or 8, fifth or sixth below eye, posterior three largest. Temporals 1+2, upper secondary largest. Ear opening vertically elliptical, lobules 3 or 4. Nuchals in four or five pairs. MBS 25–27 (mean 26·6). VS 73–76. (mean 74·3). Lamellae under fourth toe, 12–23 (mean 18·6), callose. Lowland specimens tend to have lower lamellae counts (< 20), but differ only in this respect from upland specimens.

Dorsally olive brown with moderately wide black mid-dorsal stripe. Lateral sutures of frontal light-edged. Complex pattern of light lines behind frontal on parietal region. This marking is continuous with light lines which edge mid-dorsal stripe. Three whitish lines laterally (dorsolateral, mid-lateral and lower lateral), lower two wider than uppermost line. Lateral surface black. Mid-lateral stripe not continuous over anterior margin of ear-opening, rather entering ear at or near mid-level. Lower lateral line wavy between ear and forelimb, usually reaching ear posteriorly. Broad black region between dorsolateral and mid-lateral lines usually uniformly black, although some individuals exhibit a few single anterior white spots, or, a row of widely spaced single spots. The white dorsolateral line is bordered dorsally by a narrow black band.

ETYMOLOGY. Eurydice was the wife of the mythical Greek poet Orpheus. The name was arbitrarily chosen.

HABITAT. The holotype was collected among rocks in low woodland with dense heath understory at Boonoo Boonoo Falls. The Marlaybrook specimen was collected in semi-evergreen vinethicket.

Ctenotus ingrami sp. nov.
Fig. 1. Pl. 1–3.

HOLOTYPE. QM J34792 Moombah Station approximately 60 km north-east of St George south-central Queensland. Collected during 10–12 January, 1979 by G.V. Czechura and T. Low.

PARATYPES. (Queensland) WAM R56322 11 km west of Croydon; QM J34791 Moombah Station via St George; J30438 St George; AM R96195 4.4 km from Westmar; (New South Wales) ANWC R1799, R1896–8, R2086 Fairholme Station via Nyngan; AM R16744 Mungindi; R77217, R95263 Carinda rubbish tip, Carinda.

DIAGNOSIS. A moderately large member of the *C. lesueurii*(?) group; upper labials 8; nuchals in 3 to 5 (commonly 4) pairs; snout depressed, pointed in profile; similar juvenile and adult pattern with a total of eight light lines along body; ground colour of dorsum brown; light-edged black mid-dorsal stripe present; uniformly brown head and parietal region; 19–25 callose lamellae under fourth toe; 25–27 mid-body scale rows.

DISTRIBUTION. Central Queensland and New South Wales, immediately west of the Great Dividing Range, north to Croydon (Fig. 1).

DESCRIPTION. SVL 44·9–83·7 (N = 13, mean 66·2). Length of appendages (%SVL) : TL 186·2–235·0 (N = 5, mean 204·8) : FL 23·2–29·2 (N = 13, mean 26·7) : HL 42·6–50·8 (N = 13, mean 47·9).

Snout depressed, pointed in profile. Nasals separated (occasionally in short contact). Prefrontals moderately large, separated. Supraoculars 4, first three contacting frontal. Supraciliaries 8 (rarely 9), second loreal about 1·5 times length of anterior loreal. Presuboculars 2. Postsuboculars 5–6 (mean 5·2). Upper labials 8, sixth below eye, in graded series. Temporals 1 + 2, upper secondary largest. Ear lobules 3–5 (mean 4·1). Nuchals in 3–5 pairs (commonly 4). MBS 25–27 (mean 26·0). VS 58–70 (mean 64·5). Subdigital lamellae 19–25 (mean 22·9), callose.

Dorsally olive brown with moderately wide black mid-dorsal stripe. Mid-dorsal stripe edged with lighter stripes. Dorsolateral, mid-lateral and lower lateral stripes present. Lateral surfaces black, although dorsal colour may intrude into the upper lateral zone (in some specimens almost as far as the mid-lateral stripe). Mid-lateral line bisects ear opening. Head to nuchal region uniformly olive brown. Lateral spotting or other form or patterning absent. The white dorsolateral line is bordered dorsally by a narrow black band.

ETYMOLOGY. This species is named in recognition of the contribution of Mr. Glen Ingram (Queensland Museum) to Queensland scincid taxonomy.

HABITAT. Moombah Station specimens were collected in *Acacia catenulata* forest (shrub and ground layers sparse) on stony massive earths (data from Galloway, Gunn and Pedley 1974). Fairholme station specimens were collected in an area described by Chinnick and Key (1971) as a *Eucalyptus populnea – Geijera parviflora – Capparis mitchellii* association growing on red-brown to clay loam soils where *C. ingrami* was closely associated with *Atriplex nummularia*. The Croydon specimen was collected in a *Eucalyptus miniata – Acacia* sp. association on a gravelly substrate (WAM registration data).

KEY TO *CTENOTUS* SPECIES OF SOUTHEASTERN QUEENSLAND

1a. Body pattern consisting entirely of longitudinal stripes 2
1b. Body pattern with both stripes and spots 4
2a. Ten light lines along body; ground color of dorsum black; expanded olive dorsal stripes present 3
2b. Eight white lines along body; ground color of dorsum olive brown; olive dorsal stripes absent ....*ingrami*
3a. Snout pointed in profile; mid-lateral stripe continuous over anterior margin opening or reaching near anterior margin then passing around ear opening; SVL < 60 mm ....
.... *taeniolatus*
3b. Snout rounded in profile; mid-lateral stripe reaching ear opening at mid-level — either discontinuous or passing around ear-opening from this point; SVL 56–76 mm ....*eurydice*
4a. Spots present in dorsal pattern; at least distal subdigital lamellae mucronate 5
4b. Spots absent in dorsal pattern; subdigital lamellae callose 6
5a. Mid-dorsal stripe absent; only distal subdigital lamellae mucronate ....*allotropis*
5b. Mid-dorsal stripe present; all subdigital lamellae mucronate .... *strauchii strauchii*
6a. Upper lateral zone black with single white spots present 7
6b. Upper lateral zone olive brown with paler poorly defined spots (greater than one scale deep) .... *robustus*

7a. Mid-dorsal stripe narrow and poorly defined in adults, four pale lines around body; upper lateral spots closely spaced ....*arcanus*
7b. Mid-dorsal stripe well defined; ten pale lines around body; upper lateral spots confined anteriorly or widely spaced ....*eurydice*

ACKNOWLEDGEMENTS
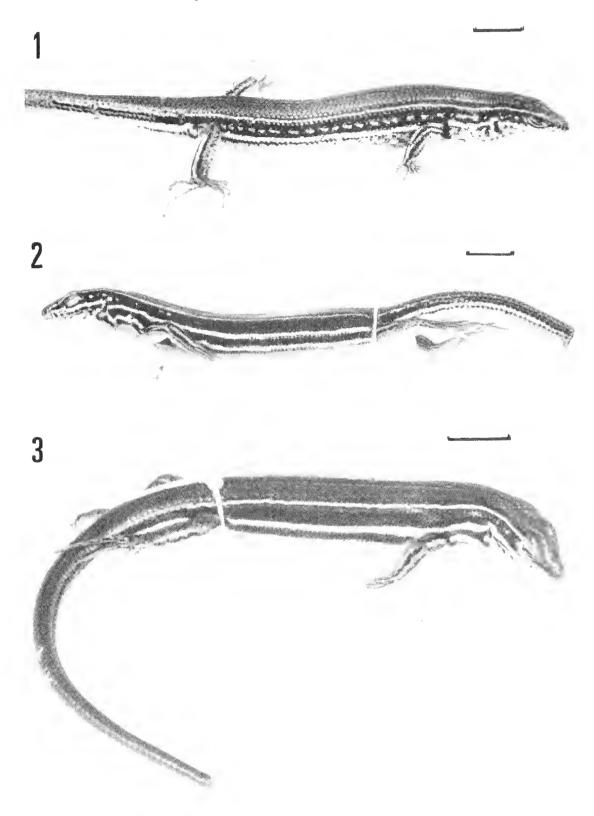
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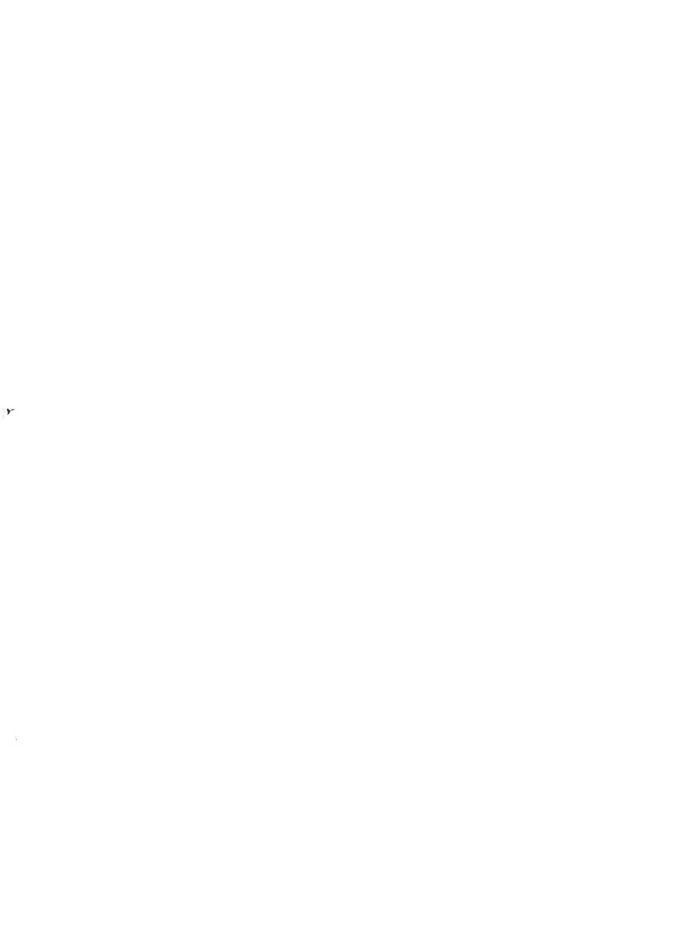
CHINNICK, L.J. and K.H.L. KEY, 1971. Map of soils and timber density in the Bogan-Macquarie Outbreak Area of the locust *Chortoicetes terminifera. C.S.I.R.O. Div. Ent. Tech. Paper* **12**.

GALLOWAY, R.W., R.H. GUNN, and L. PEDLEY, 1974. Land units, mapping units and land systems of the Balonne-Maranoa area. *C.S.I.R.O. Aust. Land Res. Ser.* **34**: 19–104.

INGRAM, G.J. and J. COVACEVICH, 1981. Frog and reptile type specimens in the Queensland Museum with a checklist of frogs and reptiles in Queensland. *Mem. Qd Mus.* **20**(2): 291–306.

SMITH, H.M., 1946 'Handbook of Lizards.' (Cornell University Press: Comstock).

STORR, G.M., 1970. The genus *Ctenotus* (Lacertilia, Scincidae) in the Northern Territory. *J. Proc. R. Soc. West. Aust.* **52**: 97–108.

1975. The genus *Ctenotus* (Lacertilia, Scincidae) in the Kimberley and North-west Divisions of Western Australia. *Rec. West. Aust. Mus.* **3**(3): 209–43.

1981. Ten new *Ctenotus* (Lacertilia, Scincidae) from Australia. *Rec. West. Aust. Mus.* **9**(2): 125–46.

PLATE 1.
1. *Ctenotus arcanus* sp. nov. (QM J38695 Mt Tewantin via Noosa, Paratype).
2. *Ctenotus eurydice* sp. nov. (AM R98372 Boonoo Boonoo Falls via Tenterfield, Holotype).
3. *Ctenotus ingrami* sp. nov. (QM J34792 Moombah Station approximately 60 km northeast St George, Holotype).
Scale equals one centimetre.

ELASMOSAURID SKULL FROM THE LOWER CRETACEOUS OF QUEENSLAND (REPTILIA: SAUROPTERYGIA).

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ABSTRACT

A nearly complete, but badly crushed skull of an elasmosaurid, probably *Woolungasaurus glendowerensis,* has been collected from near Richmond, Queensland. It is the first skull of a long-neck plesiosaur from Australia. Attribution to *W. glendowerensis* is made on the basis of associated vertebral centra. The distal portion of a very large left humerus (LO 4018) found near the Flinders River, previously provisionally attributed to *Kronosaurus,* is in fact an elasmosaurid humerus.

INTRODUCTION

The family Elasmosauridae of the suborder Plesiosauria is represented by numerous fossils from Cretaceous marine sediments in most regions, and many more or less valid genera and species have been created (Welles 1952, 1962; Persson 1963). However, most of these fossils are parts of the postcranial skeleton (vertebrae, girdle bones, limb bones etc.). As far as the author is aware from the literature, only eight specimens with skulls have been described hitherto, the one here dealt with (QM F11050) being the ninth. A tentative explanation of the scarcity of skulls is given below: the elasmosaurs were, as we know, extremely long-necked animals, so long-necked as a matter of fact that for their necks to be mobile their heads had to be small. Therefore the cranial bones were thin and delicate, and not likely to be preserved in the sediments. Besides, perhaps in many cases the heads were simply snapped off and swallowed by big sharks or carnivorous marine reptiles, such as the huge pliosaurid *Kronosaurus.* Then the headless carcasses drifted around, and when the flesh decomposed or was eaten by scavengers the bones sank to the bottom and were imbedded in the sediments.

It is true that the specimen QM F11050, because of its crushed and distorted condition, does not give much new information about the Elasmosauridae, but the facts gathered are valuable in that they corroborate our general knowledge of the family. Furthermore, the specimen is the only elasmosaurid skull known from Australia, and one of the few known from the world as a whole.

I wish to thank the Board of the Queensland Museum and the curator of geology, Dr Mary Wade, for giving me access to this unique material. I am indebted to Dr Ralph E. Molnar, editor of the *Queensland Museum Memoirs,* for stratigraphical information and for his contribution of the history of the specimen. During my young days Australia was my 'dream country' and so it still is. Hence I am particularly happy to have an opportunity to add a little contribution to the knowledge of its prehistoric fauna.

HISTORY OF THE SPECIMEN

The specimen was originally discovered by Mr T. Noonan of Maxwelton, north Queensland, in a disarticulated state in the bed of Yamborra Ck. (variously spelled) near Crowfels outstation, north of Maxwelton. Presumably the specimen had derived from the Toolebuc Fm. through which Yamborra Ck. has excavated its bed. Mr Noonan had found a block with cranial remains and a number of vertebral centra and generously donated to the Geological Survey of Queensland the cranial block and three of the vertebrae. The cranial block included the posterior two-thirds of both skull and jaws, rather distorted and crushed.

The site was later (first week of July, 1976) visited by a joint field party of R.E. Molnar, R.A. Thulborn and M. Wade, who recovered two more vertebral centra (QM F12219) and the anterior portion of a skull. R.E. Molnar (at the time at the University of New South Wales, Sydney) returned with the portion of skull to Sydney to identify it. This portion of skull eventually came to be catalogued at the Australian Museum (AM F60056). In the meantime, before the site was revisited, the posterior portion of the skull had been sent to the author for description. While at the Australian Museum the anterior portion of the skull was recognised by the Keeper of Fossils, A. Ritchie, as pertaining to the same specimen as that sent to the author. It was then transferred to the Queensland Museum and catalogued as QM F11050, and photographs were forwarded to the author. The posterior portion of the skull was then also transferred to the Queensland Museum, and, as it fitted the anterior portion, given the same number.

To clarify the convoluted history of this material here is a precis of the specimens and their catalogue numbers: skull and mandibles, QM F11050 (anterior portion previously AM F60056, posterior portion previously GSQ F10552); cervical centrum, QM F12216 (previously GSQ F10550b); a ventral impression in matrix of QM F12216 with two small pieces of bone, QM F12218 (previously GSQ F10550a); two adherent cervical centra from a position posterior and probably not adjacent to QM F12216, QM F12217 (previously GSQ F10551); and, two associated centra, not in contact, QM F12219.

COLLECTION DESIGNATIONS

AM — Australian Museum, Sydney
GSQ — Geological Survey of Queensland, Brisbane
QM — Queensland Museum, Brisbane
UCMP — University of California Museum of Paleontology, Berkeley

Order SAUROPTERYGIA
Suborder PLESIOSAURIA
Family Elasmosauridae Cope 1869
Genus *Woolungasaurus* Persson 1960

Woolungasaurus cf. *W. glendowerensis* Persson 1960

MATERIAL. Badly crushed skull and mandible in two pieces (QM F11050); 5 vertebral centra (QM F12216, QM F12217, and QM F12219); ventral impression of one centrum with bone fragments (QM F12218). See "History of the Specimen."
GEOLOGICAL HORIZON. Toolebuc Limestone (?).
LOCALITY. Yamborra Creek, near Richmond, north Queensland.

DESCRIPTION

SKULL.

As is clear from the history above it is the posterior part of the skull (QM F11050 Pl. 1) which was hitherto available to the author. The anterior part is broken off near the anterior margin of the orbits. The skull is depressed (sheared) from the left to the right side, and is so badly crushed and deformed that in most cases it is impossible to identify the sutures between the different elements, and to get accurate measurements. The entire length of the fossil, from a point in the fracture just between the anterior margins of the orbits, and to the posterior articular face of the adherent atlantoaxis, is 273 mm. The greatest breadth is 143 mm. Because of the deformation these measurements give only an approximation of the original proportions of the skull. The length of the rostral (preorbital) portion is 155 mm. Hence the length of the entire skull plus the atlantoaxis is estimated at about 42 cm.

Both orbits are strongly deformed. The lacrimal bone forms the anterolateral part of the orbital margin, and the postorbital bone forms the posterior margin. Judging from the conditions of the left orbit, which is less deformed than the right, the margin formed by the two elements mentioned was almost a semicircle. The length (i.e. the rostrocaudal diameter) of the left orbit in its present state is 78 mm. The posterior parts of both maxillae are preserved, but it is impossible to find their sutural delimitations. The frontals are strongly dislocated, pressed together, forming an elevated ridge between the orbits. Whether the frontals originally formed the dorsomedian orbital margins, as is the case in *Alzadasaurus colombiensis* Welles, 1962, or whether these margins were formed by the prefrontals cannot be seen.

Just behind the orbits is a partly covered, flat bone fragment with what seems to be a median suture. The present author has apprehended (though with some hesitation) this fragment to be the hindmost part of the frontals. If my interpretation is correct the frontals extended further posteriorly in the present species than in any other elasmosaur for which the skull is known. Only a little part of the parietals can be seen. They

had apparently a low but sharp parietal crest. Both squamosals are so badly crushed that nothing can be said about their original shape, and this is also true of the maxillae and the jugals, though the maxillary-jugal suture can be partially traced at the left side. The quadratojugals meet the jugals in an almost vertical suture. The quadratojugal-squamosal suture is, if correctly identified, situated about 8 cm above the quadrate-quadratojugal suture.

In the present species the quadrates are comparatively small bones. They are, as far as can be seen, very similar in shape to the corresponding elements of *Alzadasaurus colombiensis* (see Welles 1962, p. 19; figs. 3, 4). The right quadrate is still connected with the quadratojugal, and its articular condyle lies in its natural position towards the articular face of the mandible. Therefore the breadth of the condyle cannot be directly measured. It is estimated at 2·5 cm. The quadrate-quadratojugal suture is irregularly shaped but distinct. The left quadrate is dislocated anteriorly about 9 cm. It lies close to the median side of the left mandibular ramus, and it is partially covered by matrix and unidentified bone fragments.

Since the atlantoaxis is still in situ, the occipital condyle cannot be studied. All other elements in the occipital, basal and palatal regions of the skull are also covered, either by more or less dislocated bones or by matrix.

The hyoids are preserved. This may be only the second find of plesiosaurian ceratobranchials. The first was in the type specimen of *Alzadasaurus colombiensis* (UCMP 38349; Welles 1962, p. 21; see also Romer 1956, p. 420). The right hyoid is the better preserved. It is 101 mm. long, rod-like, and slightly curved, partly imbedded in the matrix. Its breadth is 7–8 mm. The exposed side is somewhat flattened. Both end faces have, at least as far as can be determined from what is exposed, an oval circumference and are slightly concave. Only the posteror part of the left hyoid can be seen. The parts of the mandible are, as the other remains of the cranial skeleton, crushed and deformed. The right ramus is the best preserved. Its greatest dorsoventral depth is 62 mm. At its anterior fracture its depth is estimated as 42 mm. At this point the lateromedial section is 15 mm. broad.

The angular is displaced. The supraangular-dentary suture is clearly visible, but other sutures cannot be identified with certainty.

THE DENTITION.

In the anterior portion of the skull and mandible there are 40 teeth or tooth sockets exposed (10 in the right maxilla; 11 in the left; 9 in the right mandibular ramus; 10 in the left). In the rostral portion of the skull are 32 teeth or tooth sockets. Of these 4 are in the left premaxilla and 3 in the right, 5 in the right maxilla and 4 in the left, and 8 in each dentary. Thus the animal had, if my interpretations are correct, about 18 teeth in each side of its upper jaw and about 18 in each dentary. Anyway, the number is uncertain because of the possible presence of obscured teeth and/or alveoli.

Only the crowns are exposed, and most of them are incomplete. However, it is quite clear that they do not differ from the general form from those of other elasmosaurids (and, for that matter, other dolichodiran plesiosaurians: Welles 1943, 1952, 1962; Persson 1959, 1967; and other authors). The crowns preserved are high and slender, and slightly recurved lingually and posteriorly. In parabasal section they are roughly elliptical with their labial sides somewhat less convex than the lingual ones. The ornamentation consists of delicate apico-basal ridges, which at least on the labial sides are confined chiefly to the basal part the upper part of the crown being more or less smooth. The best preserved maxillary crown has a height of 24 mm, and the height of the best preserved mandibular one is 22 mm. The basal diameters are 9·5 mm and 9 mm respectively. The teeth in the skull and mandibular portions available to me are remarkably uniform as to size, in this respect differing from the dentition in the elasmosaurs described by Welles (1943, 1952, 1962).

ROSTRAL PORTION OF THE SKULL AND MANDIBLE.

The present author has not seen this part of the specimen but has received excellent photos of it. The portion consists of the premaxillae, the anterior part of the maxillae, the nasals(?), and the rostral part of the mandibula (Pl. 1). It is, like the rest of the skull, depressed (sheared) from the left to the right. Its length from the tip of the snout to fracture is, at the approximate midline, 155 mm, and its greatest breadth (near the fracture) 143 mm. Because of the deformed state of the fossil the breadth measurement gives only a very rough idea of the original breadth.

The narial openings are strongly deformed and displaced. However, it is clear that they were comparatively small, as is the case in most of the dolichodiran plesiosaurs. They were situated about 1·5 cm before the orbits.

The premaxillae join the maxillae in a distinct suture. On the right this suture can be easily traced. It runs from the narial opening obliquely forwards and downwards and meets the alveolar line about 6 cm behind the tip of the snout. The dorsal face of the premaxillae is slightly concave, which may have given the beast a somewhat "snub-nosed" appearance. The nasals cannot be identified. Probably they are fused to the lacrimals and/or the premaxillae without a traceable suture.

The mandibular symphysis is well exposed. Its length is about 75 mm.

VERTEBRAE.

The atlantoaxis, as mentioned above, is adherent to the skull, fixed to the occipital region by matrix. Thus matrix obscures the anterior part of the atlantoaxis so its length cannot be measured. On the ventral and left lateral faces the atlantoaxial suture is visible (most of the right lateral face is obscured by matrix). The fact that the suture is not obliterated by synostosis might indicate the individual to have been fairly young but for the fusion of the cervical arches and the large size of the specimen. Since the neurapophysis is broken off the neural canal is well exposed. Its width is 12 mm. No foramina for nutritive vessels can be seen. On the ventral face there is a distinct median keel. This is highest (about 1 cm) on the atlantal part of the face, and slopes down and flattens out at the axial part. The posterior articular face is slightly concave. Its height is 31 mm and its breadth 33 mm.

Three vertebrae (QM F12216 and F12217) all of them apparently from the middle of the neck, are available for study. The measurements and indices of their centra are given in Table 1. Two adherent vertebrae both numbered F12217 are still in the natural relation to each other, held together by matrix. F12216 is the foremost of these three vertebrae. There are at least one, possibly two or more, vertebrae missing between F12217 and F12216. F12218 is not a vertebra but a piece of matrix which forms a natural cast of the ventral face of F12216.

TABLE 1: MEASUREMENTS AND INDICES OF THREE CERVICAL CENTRA OF *WOOLUNGASAURUS* CF. *W. GLENDOWERENSIS.*

	Length mm	Height mm	Breadth mm	H:L ind.	B:L ind.
QM F12216	91	75	93	82	102
QM F12217 ant.	98	85	105	86	107
QM F12217 post.	100	87	107	87	107

The neurapophyses as well as the cervical ribs are fused to the centra without any sign of a suture. In all three vertebrae the distal parts of the spinal processes and the cervical ribs are broken and lost. The width of the neural canal in F12217 is 24 mm and its height 21·5 mm. The end faces (articular faces) are slightly concave and have sharp rims. A typical feature of the anterior and middle cervical vertebrae in elasmosaurs is the presence of a pair of lateral longitudinal ridges. These ridges are distinct in all three vertebrae.

DISCUSSION

All characteristics of taxonomic value observed in the specimen are, as may readily be gathered from the literature (Welles 1943, 1952, 1962; Persson 1963; and other authors), clearly elasmosaurid. However, the generic and specific determinations are somewhat questionable. In the nearly contemporaneous *Woolungasaurus glendowerensis* Persson 1960 (a huge elasmosaur from the same region of Queensland) the major part of the skeleton is known, with the exception of the skull.

The generic and specific diagnoses are based upon features of the vertebrae, girdles and limb bones (Persson 1960, p. 11–2). Since the girdles and limbs are missing in the material here under discussion, a comparison with the *W. glendowerensis* type specimen (QM F3567) must be limited to the vertebrae. The three middle cervical vertebrae here available are all a little larger than those in the corresponding region of the type specimen (Persson 1960, p. 13, table 4), but the proportions of their centra are very similar to those of the holotype (cf. Table 1). The two later-found vertebrae (QM F12219) look indistinguishable from the type vertebrae of *Woolungasaurus glendowerensis* (Molnar, pers. comm. 1981). In view of these facts the author supposes the Yamborra specimen to belong to the genus *Woolungasaurus* Persson 1960 and, with reservation, to the type species, *W. glendowerensis.*

As mentioned in the introduction, relatively few skulls of elasmosaurs are known and most of them, like the present one, are crushed and more or less deformed. As a consequence detailed discussion is of little value. If my interpretation of the skull bone fragments is correct the frontal bones extended further posterior in the present form than in any other elasmosaur for which the skull has been described. This would possibly be of taxonomic interest.

The unusual uniformity in size of the teeth of the specimen here described has probably no taxonomic significance. Perhaps we are seeing a consequence of sexual dimorphism, one sex (♀?) having a rather uniform dentition, the other a more irregular one, with a few large, more or less tusk-like teeth among the others in the rows. The occurrence of this specimen (QM F11050, QM F12216-9) in the Toolebuc Fm., while the holotype of *W. glendowerensis* is from the underlying Wallumbilla Fm. is not considered to be of significance.

Family Elasmosauridae Cope 1869
Woolungasaurus? sp.

MATERIAL. Distal part of left humerus, in the Paleontological Institute of the University of Lund, Sweden; Cat. no. LO 4018. Previously described as indeterminable by the author (Persson 1960, p. 20).

GEOLOGICAL HORIZON. Probably Albian (probably either Toolebuc Fm. or Allaru Mudstone).

LOCALITY AND FIND HISTORY. In 1958, the author saw the fossil for the first time. It then lay in a stone heap ('rock garden') at Boree Park stn near Richmond, Queensland. A few years earlier it had been collected from a limestone outcrop near the Flinders River by Mr W. Graw, then owner of the station. Mr Graw generously presented the fossil to the University of Lund, Sweden.

DISCUSSION

Courtesy of the Queensland Museum, Brisbane, the author has received an excellent cast of the right humerus of the *Woolungasaurus glendowerensis* type specimen (QM F3567). LO4018 (pl. 2, Fig. 1) is part of a somewhat larger bone than the type humerus, but there are no observable differences of taxonomic value. However, the elasmosaurid propodial bones are, as we know, of very generalized form. Hence, it would be unwise to refer without reservation a fossil like this to a given genus or species unless associated with other skeletal material.

In my paper of 1960 I wrote: 'Specimen LO4018 must have belonged to a very large Plesiosaurian, possibly *Kronosaurus*'. As follows from the discussion above the fossil cannot have belonged to *Kronosaurus* or any other pliosaur. There is no doubt about its elasmosaurid affinity. Since *Woolungasaurus* is the only elasmosaurid genus from this region hitherto adequately documented it seems appropriate to refer the present specimen, at least tentatively, to this genus.

LITERATURE CITED

PERSSON, P.O. 1960. Lower Cretaceous Plesiosaurians (Rept.) from Australia. *Lunds Univ. Årsskr.* N.F. Avd. 2. **56** (12): 1–23. Also as *Kungl. Fysiogr. Sällsk. Handl.* N.F. **71** (12): 1–23. Pls. 1–3.

— 1963. A revision of the classification of the Plesiosauria with a synopsis of the stratigraphical and geographical distribution of the group. *Lunds Univ. Årsskr.* N.F. Avd. 2. **59** (1): 1–59.

ROMER, A.S. 1956. 'Osteology of the Reptiles'. (Chicago: Univ. of Chicago Press) p. 687. Figs. 1–248.

WELLES, S.P., 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. *Mem. Univ. Calif.* **13** (3): 125–215. Figs. 1–37. Pls. 12–29.

— 1952. A review of the North American Cretaceous elasmosaurs. *Univ. Calif. Publ. Geol. Sci.* **29**(3): 47–144. Figs. 1–25.

— 1962. A new species of elasmosaur from the Aptian of Colombia and a review of the Cretaceous plesiosaurs. *Univ. Calif. Publ. Geol. Sci.* **44** (1): 1–96. Figs. 1–23. Pls. 1–4.
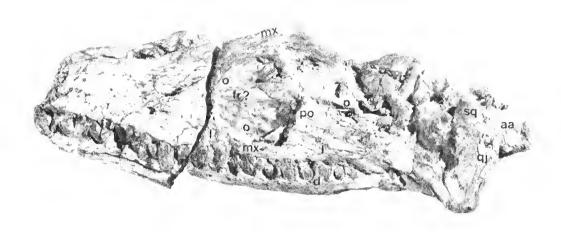
PLATE 1
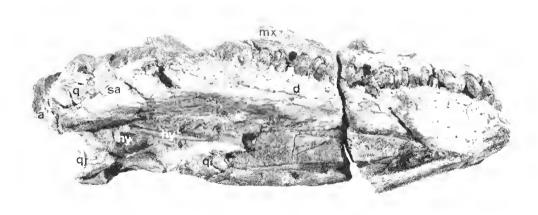
WOOLUNGASAURUSCF W. GLENDOWERENSIS

FIG 1. Skull and mandibula of *Woolungasaurus* cf. *W. glendowerensis* (QM F11050), in anterolateral aspect.

FIG 2. The same in ventrolateral aspect. Abbreviations: a, articular; aa, atlantoaxis; d, dentary; fr, frontal; hy, hyoid; j, jugal; l, lacrimal; mx, maxilla; o, orbit; p, parietal; po, postorbital; q, quadrate; qj, quadratojugal; sa, supraangular; sq, squamosal.
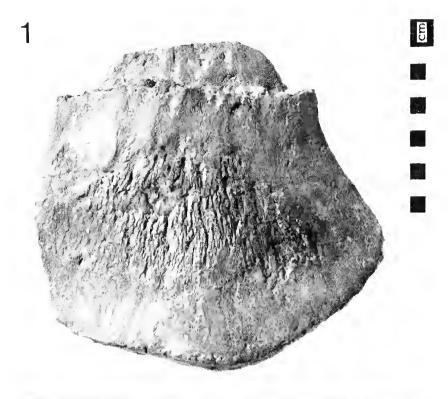
1

2

cm.

PLATE 2
FIG. 1. *Woolungasaurus?* sp. (University of Lund LO4018), distal portion of left humerus in lateral aspect.
FIG. 2. Model of *Woolungasaurus glendowerensis*, prepared by the author.

PLATE 2

PALLIMNARCHUS AND OTHER CENOZOIC CROCODILES IN QUEENSLAND

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ABSTRACT.

Pallimnarchus pollens is a valid crocodilian taxon, based on a lectotype (articulated dentaries) selected in this paper. Much material that has been referred to *P. pollens* is attributable to *Crocodylus porosus* or is indeterminate at present. *Crocodylus nathani* is a junior subjective synonym of *C. porosus*. Both *P. pollens* and *C. porosus* date back into the Pliocene *(P. pollens* in the Chinchilla Sand and *C. porosus* in the Allingham Fm). *C. porosus* remains, including the material from 'Lansdowne' near Tambo previously referred to *P. pollens,* indicate a former range into the interior waterways of Queensland. There is no recognizable fossil material of *C. johnsoni*. A dentary fragment from near Murgon (S.E. Qld) resembles material from the Etadunna and Waite Fms. of central Australia.

INTRODUCTION

Late last century de Vis (1886) recognized a large extinct Queensland crocodilian that appeared to differ from living crocodilians in the possession of a broad snout and imbricated dermal scutes. De Vis informally designated this beast *Pallimnarchus pollens,* and he and H.A. Longman (1925, 1926) carried out further work on it. The name gained widespread useage in the Australian secondary and popular literature (e.g. Jack and Etheridge, 1892; Lascron, 1950; Mincham, 1967). More importantly, much Plio-Pleistocene crocodilian material, especially in the Queensland Museum collections, has been referred to this taxon.

Longman (1924) described *Crocodylus nathani,* to which further material was never referred. Much of the material referred to *P. pollens* and the *C. nathani* specimen appeared to be indistinguishable from *Crocodylus porosus.* Type material was never designated for either of these two species.

The present study nominates lectotype material for both *P. pollens* and *C. nathani*. As the descriptions of de Vis and Longman are largely accurate and comprehensive, little further detailed description is presented here: however some material is newly illustrated with photographs. Much material of *Pallimnarchus* has been referred on the form of the armour. This is not discussed here because no armour is unambiguously associated with the lectotype material, and a collection of modern material sufficient for

comparison and study of variation is not available to me. Nor is the generic status of *Pallimnarchus* discussed, pending study of a similar Miocene crocodilian from South Australia. The lectotype material is more restricted than that used by de Vis (1886) in forming his concept of *Pallimnarchus,* indeed that material (see below) probably pertains to three distinct taxa. Since the extent of differences from *Crocodylus* cannot be adequately assessed, the genus *Pallimnarchus* is herein tentatively accepted.

In addition to *P. pollens* and *C. nathani,* a probably Miocene crocodile dentary fragment from near Murgon, southeast Queensland, is described and illustrated to round out this study of fossil crocodilian material from Queensland. Ziphodont crocodilians, recently studied (Molnar, 1981) are not discussed.

Pallimnarchus pollens de Vis 1886

PREVIOUS WORK.

De Vis (1886) listed and described crocodilian material presumably from 'the Condamine drift' (1886, p. 182) to which was appended 'The cabinet name, *Pallimnarchus pollens* . . . (as); merely one of convenience.' (de Vis, 1886, p. 191). This name however has been subsequently treated as both valid and formally proposed (e.g. Jack and Etheridge, 1892; Longman, 1925; Steel, 1973). There has been no restudy of de Vis' material, Longman (1925; 1926) having referred to it only

insofar as relevant to the description of newly discovered material, so that this study constitutes the first revision of de Vis' taxon.

De Vis did not designate a type specimen for *Pallemnarchus pollens,* but described together material from four (possibly five) individuals of at least two, probably three, different taxa. De Vis' intention with regard to the type material cannot be deduced from the labels or the register entries, as the former treat all the specimens described by de Vis (1886), with the exception of the maxillary piece, as syntypes, while the register designates QM F1149 (two articulated dentaries) as the type. The maxillary piece figured by de Vis (1886, pl. X) was not recognised in the collections.

DESIGNATION OF LECTOTYPE OF *P. POLLENS.*

QM F1149 (Pl. 1, Figs. A,B) is the most complete of the specimens used by de Vis in the original description of *P. pollens,* and was figured by him (de Vis, 1886, pl. 10, fig. 1). This specimen matches both description and illustration, so there can be no doubt that QM F1149 is in fact the specimen used by de Vis. It also best illustrates the distinctive features of the taxon, and thus is here designated the lectotype. It includes the anterior portions of both dentaries, fused at the symphysis and lacking all but two teeth. This number also includes a fragment of the left angular not sharing any contact with the dentaries, but of appropriate size and preservation to pertain to the same individual. This angular (Pl. 2, Fig. 1) differs from that of *Crocodylus porosus,* but is generally similar to the corresponding portion of the angular of *Crocodylus johnsoni.* In view of this similarity, and in the absence of any evidence of association

between these pieces, the angular has been re-registered as QM F11610: nonetheless it is possible that it does pertain to the lectotype specimen of *P. pollens.*

The type jaws of *P. pollens* represent an immature individual, probably about three metres long (judging from comparison with *C. porosus).* The current disposition of the remaining material discussed by de Vis (1886) is given in Table 1. The only locality information for any of these specimens is that given by Jack and Etheridge (1892) and they do not indicate which specimens came from which localities. One of the listed localities (Eight Mile Plains) is at Brisbane, one (Gowrie Ck.) is on the eastern Downs, two (Wiembilla Ck., Chinchilla) on the western Downs, and the last (Condamine River) traverses both eastern and western Downs. Because de Vis (1886) implied that the specimens came from the Downs, and because their preservation is consistent with such an origin, it is assumed that the lectotype derives from the Pliocene or Pleistocene sediments of the Darling Downs.

Order: CROCODILIA
Suborder: EUSUCHIA Huxley
Family: Crocodylidae Cuvier
Genus: *Pallimnarchus* de Vis 1886

TYPE SPECIES: *Pallimnarchus pollens* de Vis 1886.

DIAGNOSIS: As only a single species is attributed to this genus the generic diagnosis cannot be separated from the specific diagnosis.

TABLE 1: DISPOSITION OF DE VIS' (1886) CROCODILIAN MATERIAL

Elements	Specimen	Taxon	Comments
anterior portions of both mandibles	QM F1149	*P. pollens*	Here designated the lectotype
angular, incomplete	QM F11610	*P. pollens?*	Initially numbered QM F1149 (see text)
symphyseal portion of left mandible	QM F1155	*P. pollens*	See text
incomplete right surangular	QM F1150	*C. porosus*	Shows no distinction from *C. porosus*
incomplete left premaxilla	QM F1151	*P. pollens?*	See text
posterior part of maxilla	?	?	Not recognized
left jugal	QM F1152	*Q. fortirostrum?*	See Molnar (1981)
anterior portion of skull roof	QM F3303	*C. porosus?*	See text
incomplete right quadrate	QM F1160	*P. pollens?*	See text

Species: *P. pollens* de Vis 1886
Pallimnarchus pollens de Vis 1886 *partim.*
Pallimnarchus pollens de Vis 1907 *partim.*
Pallimnarchus pollens Longman 1926, but not
Pallimnarchus pollens Longman 1925.

LECTOTYPE SPECIMEN: QM F1149. Anterior
portions of both dentaries, articulated at the
symphysis (Pl. 1, Figs. A, B).

LOCALITY: Unknown, probably on the Darling
Downs southeast Queensland.

HORIZON: Unknown, probably Pliocene or
Pleistocene.

DIAGNOSIS: Symphyseal portion of mandibles
broader than in any living species of *Crocodylus;*
angle between ramus of mandible and plane of
symphyseal surface greater than in either *C.
porosus* or *C. johnsoni.*

REFERRED MATERIAL: QM F11612, Chinchilla
Sand, Chinchilla, late Pliocene; QM F1538,
unknown age, Leichhardt River; QM F1155,
Pleistocene?, eastern Downs?; AM F36947,
Pleistocene?, Gregory River?, all of which are
symphyseal portions of dentaries; and, QM F2025,
Pleistocene?, Macalister, half of right dentary.
Material probably referable to *P. pollens:* QM
F1151, Pleistocene?, eastern Downs?; QM F1154,
Chinchilla Sand, Chinchilla, both premaxillae,
late Pliocene; QM F1160, Pleistocene?, eastern
Downs?; QM F1166, Chinchilla Sand, Chinchilla,
Late Pliocene, both quadrates; and, QM F1165,
unknown age, unknown locality, the anterior
portion of a dentary. Contrary to my previous
belief (Molnar, 1981, p. 824) there is no evidence
for a second non-ziphodont crocodile at
Chinchilla.

COMPARISON.

MANDIBLES. As noted by de Vis the mandibles of
Pallimnarchus give the immediate impression of
being broader than those of *C. porosus* (and much
broader than those of *C. johnsoni* or *C.
novae-guineae).* All of the sufficiently well
preserved Plio-Pleistocene mandibles were mea-
sured, together with those of available modern
Australasian crocodilians (Table 2), to allow
comparison. The following characters were used in
the comparison: i, alveolar diameters; ii,
interalveolar distances; iii, position of anterior end
of splenial with respect to toothrow; iv, position of
posterior end of symphysis with respect to

toothrow; v, angle of divarication of the
mandibles, and; vi, an index of the length to
breadth ratio of the symphyseal platform.

Characters i to iv revealed no consistent
differences between *P. pollens* and *C. porosus;* but
the last two characters were clearly different. The
angle of divarication was taken to be the angle in
the horizontal plane between the symphyseal
surface and the medial surface of the mandibular
body. Since many of the fossil specimens had been
disarticulated at the symphysis, the angle was
measured separately for each side. These angles
are given in Table 3. As some of the fossil jaws
were lacking the anterior extremity of the first

TABLE 2: MATERIAL EXAMINED
Crocodylus porosus
  AM R32645
  AM R 71296
  AM R71297
  AM R71298
  AM S1671
  NMV 58499
  NMV D55277
  NMV R1580
  NMV R4224
  NMV R9920
  QM F1161 *
  QM J5005
  QM J13443
  QM J22550
  QM J24495
  QM J28902
  QM J29021
  QM J39231
  QM J39232
  QM J39233
  QM J39283
  QM J39284
Crocodylus johnsoni
  QM J4280
  QM J4281
  QM J22551
  QM J28895
  QM J29021
  QM J29022
  QM J39230
Crocodylus novae-guineae
  QM J5332
  QM J5664
Pallimnarchus pollens
  AM F36947 *
  QM F1149 *
  QM F1155 *
  QM F1538 *
  QM F2025 *

AM, Australian Museum, Sydney; NMV, National
Museum of Victoria, Melbourne; QM, Queensland
Museum, Brisbane: *, fossil material.

alveolus, rather than use the anteroposterior length of the symphysis in determination of the length to breadth ratio of the symphyseal platform, the distance from the posterior extremity of the symphysis (sometimes on a low genial tubercle) to the nearest portion of the first alveolus was used (Fig. 1). This allowed a larger sample for comparison. This index of length was plotted against the maximum breadth of each dentary at the symphyseal platform, from the symphyseal surface to the lateral margin (invariably at the fourth alveolus) and the results are given in Fig. 1. Again the individual dentaries were measured because of disarticulation of the fossil material.

Both characters verify that the mandibles of *P. pollens* are distinctly broader than those of *C. porosus*. Indeed for the length: breadth index, *P. pollens* is as distinct from *C. porosus* as is the latter from *C. johnsoni*. The wide range of sizes for *C. porosus* implies considerable age variation. These characters clearly distinguish *P. pollens* from *C. porosus* and *C. johnsoni*, and by implication, from *C. novae-guineae* (for which an

TABLE 3: ANGLE OF DIVARICATION OF DENTARY RAMUS FROM SYMPHYSEAL SURFACE

Taxon	Number	Side	Angle (°)
C. porosus	NMV D55277	r	17
C. porosus	NMV D55277	l	15
C. porosus	NMV R1580	r	14
C. porosus	NMV R1580	l	12
C. porosus	NMV R4224	r	22
C. porosus	NMV R4224	l	20
C. porosus	QM J5005	r	17
C. porosus	QM J5005	l	17
C. porosus	QM J22550	r	18
C. porosus	QM J22550	l	17
C. porosus	QM J28902*	r	21
C. porosus	QM J28902*	l	18
C. porosus	QM J39231	r	16
C. porosus	QM J39231	l	18
C. porosus	QM J39232	r	18
C. porosus	QM J39232	l	16
C. porosus	QM J39233	r	19
C. porosus	QM J39233	l	16
P. pollens	QM F1149**	r	23
P. pollens	QM F2025	r	26

* juvenile specimen

**lectotype

adequate number of specimens was not available) which has a narrower snout and jaws than *C. porosus*.

CRANIAL MATERIAL. Of the original cranial material assigned to *P. pollens* by de Vis, the posterior portion of the maxilla (1886, pl. X, fig. 2) was not located, and the jugal has been discussed elsewhere, and assigned to *Quinkana* or a similar form (Molnar, 1981). The Lansdowne snout, assigned to *P. pollens* by Longman (1925) will be discussed later. This leaves the frontals (QM F3303), the premaxilla (QM F1151), and the incomplete quadrate (QM F1160) as the only remaining cranial material referred to *P. pollens* in the literature.

The fused right and left frontals (QM F3303) are preserved with a small portion of the left postorbital and the greater portion of the right lachrymal (Fig. 2). Anteriorly the back extremities of the nasals are present. The portion preserved is generally like the corresponding portion of *C. porosus*. There is a low lachrymal ridge, but the orbital margins are not raised and a distinct medial sulcus runs anteriorly along the nasals. The lachrymal ridge is characteristic of *C. porosus*, in which the orbital margins are usually (but not always) elevated. I have never seen a nasal sulcus on a specimen of *C. porosus*. In view of the presence of the lachrymal ridge, and the limited sample of *C. porosus* available, it is not

FIG 1   Graph of half-breadth of symphyseal region (B) against index of symphyseal length (L). Squares indicate values for *Pallimnarchus pollens*, triangles for *Crocodylus porosus*, and discs for *Crocodylus johnsoni*. Values for right and left sides of one individual are linked by dashed line. Inset shows dimensions measured. See text for further comment.

possible to be confident that this specimen pertains to *P. pollens* rather than to *C. porosus*.

The left premaxilla (QM F1151) is lacking only the anterior portion back to the second alveolus. It differs from premaxillae of *C. porosus* in having a transverse posterior narial margin, those of *C. porosus* being inclined posteriorly (Fig. 3). Thus it seems likely that this specimen is referable to *P. pollens*.

The right quadrate (QM F1160) is incomplete anteriorly, lacking almost half of its full length. It differs from the corresponding portion of the quadrate of *C. porosus* in two character states. In ventral aspect the lateral margin proceeds anterolaterally from the lateral condyle, rather than anteriorly as in *C. porosus* (Fig. 4). In *C. porosus* the exoccipital buttress is never removed from the medial condyle by a distance exceeding the total width of the condyles (Table 4). In QM F1160 (Pl. 2, Fig. 10) however the distance from medial condyle to exoccipital buttress exceeds the total width by 24 per cent. This character state also distinguishes this quadrate from those of *C. johnsoni* and *C. novae-guineae*

available. Thus it seems likely that QM F1160 is also referable to *P. pollens*.

These latter two specimens are referred to *P. pollens* because they differ in form from living Australasian crocodilians. They yield no compelling indication of relationship to any ziphodont form (i.e. *Quinkana*). Nonetheless in the absence of positive evidence of their association and pending discovery of articulated crania of *Pallimnarchus*, this assignment is tentative.

THE LANSDOWNE SNOUT. Originally described by Longman (1925) this snout (QM F1752) together with fragments of the postorbital region of the skull, jaws and postcranial skeleton, was found on 'Lansdowne', near Tambo, south central Queensland. The snout appears exceptionally broad and was thus assigned to *P. pollens*. In fact the ratio of the interorbital distance to the orbitopremaxillary distance is matched by some large modern specimens of *C. porosus* (G. Webb, pers. comm., 1978). This has led to re-evaluation of the taxonomic position of this specimen.
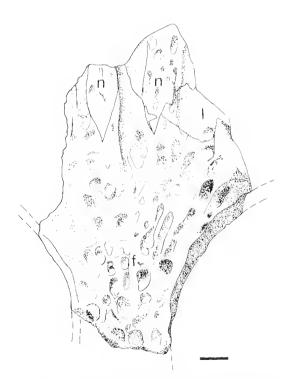
FIG. 2 Frontals and associated elements initially referred to *Pallimnarchus pollens* (QM F3303), in dorsal aspect, anterior to the top. f, frontals; l, lachrymal; n, nasal. Bar represents 1cm.
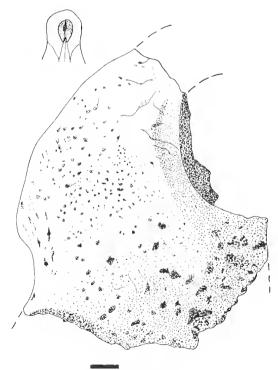
FIG 3 Left premaxilla referred to *Pallimnarchus pollens* (QM F1151) in dorsal aspect, anterior to the top. Inset shows form of premaxillae, and external nares in *Crocodylus porosus*. Bar represents 1cm.

Longman based his assignment of the Lansdowne material to *Pallimnarchus* also on the similarity of the premaxillae to that assigned by de Vis to *Pallimnarchus* (QM F1151). However, the Lansdowne premaxillae differ from QM F1151 in the same character state as do those of *C. porosus*, namely the inclined posterior margin of the external nares (cf. Longman, 1925 fig. 1). At least one other character state of the Lansdowne snout is matched in *C. porosus*. Although the dorsal surface of the snout is crushed, especially posteriorly, and (perhaps because of this) there is no indication of either lachrymal ridge, the sulci bounding the central ridge are present (cf. Molnar, 1979). They are subdued but this is typical of the large specimens of *C. porosus* in the QM collections.

Additionally the *P. pollens* mandible (QM F2025) from Macalister, southeast Queensland, (Longman, 1926) that matches the Lansdowne snout in size, suggests that this snout is not from *P. pollens*. When the symphyseal surface of the dentary is placed in the plane of the medial junctions of the premaxillae and maxillae, to approximate the position of the dentary in life, the rear portion of the dentary projects laterally well beyond the lateral margin of the skull (Fig. 5). Because of the snout proportions, external narial form, sulci, and lack of match with QM F2025 the Lansdowne snout is considered to represent *C. porosus* and not *P. pollens*.

OTHER REFERRED MATERIAL. Other specimens in the Queensland and Australian Museums clearly pertain to *P. pollens*. Noteworthy among this material is the dentary from Macalister (QM F2025) already mentioned. A left premaxilla (QM F1154) from Chinchilla exhibits the same transverse orientation of the posterior narial margin found in QM F1151, and hence probably derives from *Pallimnarchus*. There is also an almost complete, elongate left quadrate (QM F1165) from the Chinchilla Sand (Pl. 1, Figs, G, H). Although the lateral condyle is worn, the margin anterior to it projects laterally, unlike the condition in *C. porosus*, and the exoccipital buttress is well removed from the medial condyle (Table 4), thus matching QM F1160 referred probably to *Pallimnarchus*. Among the relatively plentiful maxillary and cranial material in the Queensland Museum none is clearly referable to *P. pollens*.

FIG. 5 The Macalister mandible *(Pallimnarchus pollens,* QM F2025) in outline, superimposed on the outline of the Lansdowne snout (QM F1752). With the symphyseal surface of the jaw aligned with the medial plane of the snout, the jaw can be seen to project posteriorly beyond the lateral margin of the skull to a degree exceeding that found in modern crocodilians. This (together with other evidence) suggests that the snout does not derive from *P. pollens*. Hatched areas represent plaster reconstruction. Note that the skull is reversed.

FIG. 4 Quadrates of *Pallimnarchus pollens* (A) and *Crocodylus prorosus* (B) in outline in ventral aspect. Note difference in lateral outline. A drawn from QM F1162 and QM F1165, and B drawn from QM J13443. Not to scale.

CROCODYLUS NATHANI LONGMAN

The species *C. nathani* was erected by Longman (1924) for the reception of three dentary pieces and an incomplete cranial roof from Tara Creek, east central Queensland. To his new species, Longman also referred the symphyseal portion of a dentary (QM F1538) from the Leichhardt River, northwest Queensland. This is presumably the mandible mentioned by de Vis (1907), as *P. pollens*. The material from Tara Creek includes two portions of the anterior region of dentary (QM F1512, QM F1513) and a segment from the middle part of the jaw (QM F11609) believed by Longman to be 'probably continuous in life with F. 1512' (Longman, 1924, p. 24) and so registered at the time. The incomplete cranial roof (QM F1514) includes both frontals, portions of both laterosphenoids, and a small part of the left postorbital (Fig. 6).

Longman did not designate a holotype of *C. nathani*, but indicated that the diagnostic characters were found in the symphyseal region of the dentary, thus limiting possible type specimens to QMF1512 (Pl. 2, Figs. E, F) and QM1513 (Pl. 2, Figs. A, B.) Of these QM F1513 is the (slightly) more complete and the better preserved, and is here designated the lectotype.

Order CROCODILIA
Suborder EUSUCHIA Huxley
Family Crocodylidae Cuvier
Genus *Crocodylus* Laurenti 1768
Species *C. nathani* Longman 1924

LECTOTYPE SPECIMEN: QMF1513. Anterior portion of left dentary lacking the anterior extremity (Pl. 2, Figs. A, B).

TABLE 4: DIMENSIONS OF THE POSTERIOR MOEITY OF THE QUADRATE.

Taxon	Number	Side	Condylar width(mm)	Distance from int. condyle to exoccipital buttress (mm)	Distance to buttress as percentage of width
C. johnsoni	QM J4280	r	19	16	84
C. johnsoni	QM J4280	l	19	13	68
C. johnsoni	QM J22551	r	22	17	77
C. johnsoni	QM J22551	l	22	16	73
C. johnsoni	QM J28895	l	25	16	64
C. johnsoni	QM J28895	i	25	20	80
C. johnsoni	QM J39230	r	35	26	74
C. johnsoni	QM J39230	l	33	30	91
C. novaeguineae	QM J5332	r	24	17	71
C. novaeguineae	QM J5332	l	23	18	78
C. novaeguineae	QM J5664	r	30	24	80
C. porosus	QM J5005	r	81	57	70
C. porosus	QM J5005	l	75	62	83
C. porosus	QM J13443	r	44	35	80
C. porosus	QM J13443	l	43	36	84
C. porosus	QM J22550	r	41	37	90
C. porosus	QM J22550	l	40	36	90
C. porosus	QM J29021	r	18	13	72
C. porosus	QM J29021	l	19	15	79
C. porosus	QM J39231	r	38	34	89
C. porosus	QM J39231	l	38	31	82
C. porosus	QM J39232	r	38	37	71
C. porosus	QM J39233	r	37	31	84
C. porosus	QM J39233	l	38	30	79
C. porosus	QM J39283	r	77	63	82
C. porosus	QM J39283	l	71	60	85
C. porosus	QM J39284	r	77	69	90
C. porosus	QM J39284	l	78	76	97
C. porosus	QM F1161	l	72	52	72
P. pollens?	QM F1160	r	66	82+	124+
P. pollens?	QM F1165	l	55	68	124

LOCALITY: Tara Creek, northeast Queensland.

HORIZON: Not recorded.

AGE: Probably Pliocene.

DIAGNOSIS: '... the mandibular symphysis ... extends barely parallel to the posterior border of the fourth tooth.' (Longman, 1924, p. 23).

To my knowledge this taxon was never again cited in the primary literature until I suggested it to be a synonym of *C. porosus* (Molnar, 1979), and no further material has been referred to it.

Longman distinguished this species from the other species of *Crocodylus* (and from *Pallimnarchus pollens*) using the position of the posterior end of the symphysis vis-a-vis the toothrow. He also suggested that the enlarged central dentary teeth were the eleventh and twelfth, rather than the tenth and eleventh as in *C. porosus* (Longman, 1924). This latter suggestion was based on his assumption that QM F11609 was continuous with QM F1512: this, however may be questioned. QM F1512 (and QM F1513) have the splenial so well fused to the dentary that no trace remains of its suture with that element, while on QM F11609 the splenial was so loosely attached that it has become separated from the dentary and lost. This indicates that these two specimens derive from two different individuals. There is no contact between the two specimens, and hence there is no evidence that the eleventh and twelfth were the enlarged dentary teeth rather than the tenth and eleventh.
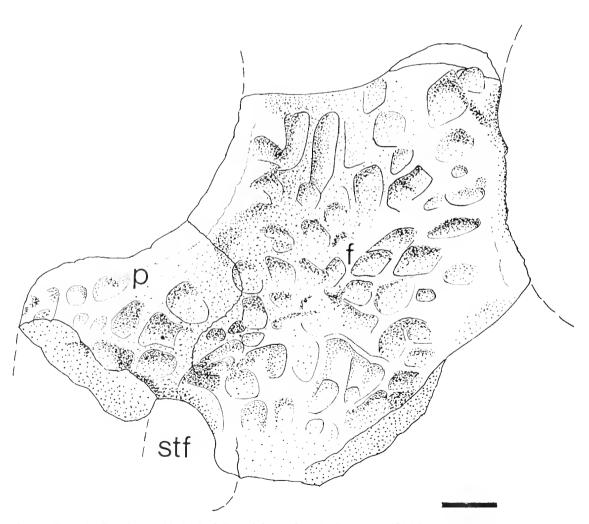
FIG. 6   Frontals (f) and postorbital (p) of *Crocodylus nathani* (= *C. porosus*) (QM F1514) in dorsal aspect, anterior to the top. stf, supratemporal fenestra. Bar represents 1 cm.

Examination of the *C. nathani* dentaries (QM F1512, QM F1513) revealed the disconcerting circumstance that while Longman's photographs (1924, Pl. 3) clearly represent these two specimens, and clearly show that the posterior end of the symphysis is at the level of the fourth alveolus (and indeed well anterior to the posterior border of that alveolus) the specimens themselves show nothing of the kind. When the symphyseal surface of either of these specimens is placed against one edge of a T-square the perpendicular edge clearly intersects the fifth (not the fourth) alveolus (Fig. 7). Hence this feature cannot distinguish *C. nathani* from either *C. porosus* or *P. pollens*. The explanation of the deceptive appearance of the photographs was clarified by rotation of the specimens about their longitudinal axes: when photographed the specimens were not viewed in dorsal aspect. Instead they were photographed from a direction of about 45 degrees lateral to the vertical. This has obscured from view the more ventral part of the symphysis and given the appearance that the symphysis terminated posteriorly at the fourth alveolus.

Unfortunately neither QM F1512 nor QM F1513 is sufficiently well preserved anteriorly to permit comparison using the length: breath ratio discussed for *P. pollens*. The position of the symphysis is not distinctive, nor is there convincing evidence that the enlarged dentary teeth were different from those of *C. porosus*. In sum, no character states distinguish *C. nathani* from *C. porosus*, and thus *C. nathani* Longman becomes a junior subjective synonym of *C. porosus*.

The cranial roof fragment (QM F1514) referred to *C. nathani* consists of the greater portion of both frontals, fused at the midline, and much of the left, but only a bit of the right laterosphenoid. The left postorbital is represented by the upper portion contributing to the skull roof. The orbital margins are strongly raised as in *C. porosus*, and the sculpture of the roof closely resembles that found in that species. This piece cannot be distinguished from the corresponding portion of the skull of *C. porosus*.

The worn symphyseal region of a left dentary (QM F1538) from the Leichhardt River, referred to *C. nathani* by Longman, matches in length: breadth index other specimens referred to *P. pollens* (Fig. 1) and thus is regarded as pertaining to that species (as de Vis had believed).

CROCODYLUS POROSUS FOSSILS

Jack and Etheridge (1892) list several sites yielding fossil material of *C. porosus*. Although I have seen none of this material, other material in the Queensland Museum, in addition to the Lansdowne snout (QM F1752), may be attributed to (i.e. cannot be distinguished from) *C. porosus*. This material comprises a partial dentary from Macalister (QM F11611), a premaxilla from the Condamine River (QM F11626), and the previously described incomplete snout, (QM F9229; Molnar, 1979) and a much larger, incomplete dentary (QM F11623) both from the Allingham Fm. The partial dentary from Macalister, as well as that from the Allingham Fm., consists of the anterior portion lacking the anterior end. Both are markedly narrower in the symphyseal region than those of *P. pollens* (Pl. 1, Figs E,F). The Condamine premaxilla matches those of *C. porosus* in the inclination of the posterior margin of the external narial opening.

The Allingham material reinforces the conclusion that *C. porosus* was already present in Australia during the Pliocene (Molnar, 1979). The distribution of the material, particularly at Macalister and Tambo, also suggests that *C.*

FIG. 7 Lectotype mandibular segment of *Crocodylus nathani* (=*C. porosus*) (QM F1513) in dorsal (A) and anterior (B) aspects, to illustrate orientation of specimen for plate 3 of Longman (1924). A, mandibular segment in dorsal aspect showing 5th mandibular alveolus at level of posterior end of symphysis (note that the discrepancy in position of the end of the symphysis between this figure and Pl. 2, B of this paper is due to parallax in the photograph). B, mandibular segment in anterior aspect showing direction of view (m) for Fig 7A and Pl. 2, B of this paper and that (1) for pl. 3 of Longman (1924) (1). See text for further comment.

porosus once enjoyed a considerably wider range than at present extending well into the interior of Queensland. The occurrence of material attributable to both *P. pollens* and *C. porosus* at Macalister suggests that their ranges may have overlapped, although in the absence of detailed stratigraphic information this must remain only a suggestion. The presumably Pleistocene Sand at Macalister differs both from the Chinchilla Sand and the other fluviatile deposits of the eastern Downs (Woods, 1960) so the stratigraphic relations of this bed to other deposits is unclear.

THE MURGON CROCODILE

The symphyseal region of the left dentary (QMF11625) of a small crocodilian (Pl. 2, Figs. G, H) from near Murgon, southeast Queensland, differs in general form and proportions from those of *C. porosus, C. johnsoni, C. novae-guineae* and *P. pollens*. Unfortunately the first alveolus is broken medially, so that the length:breadth index used for comparison of *P. pollens* cannot be obtained for this specimen. The symphyseal region is subtriangular in dorsal aspect, rather than subrectangular as in *C. porosus,* or broadly rounded as in *P. pollens* (Fig. 8). The symphysis ends posteriorly at the level of the seventh dentary alveolus, farther back than in either *C. porosus* (the fifth) or *P. pollens* (the fifth or sixth). In *C. novaeguineae* the back of the symphysis is at a level between the sixth and seventh alveoli, but the form of the symphyseal region is more like that of *C. porosus.*
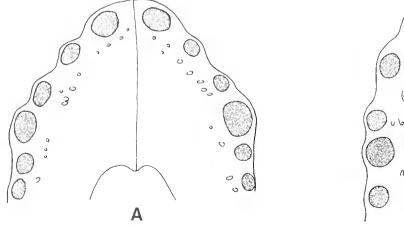
Viewed from above this fragment resembles a specimen from the Waite Fm. (Woodburne, 1967), and also the corresponding region of the dentary of a form, under study, from the Etadunna Fm. It differs from both of these, however, in the position of the back of the symphysis, which in both Etadunna and Waite forms is at the level of the fifth dentary alveolus.

The Murgon fragment presumably derives from the Oakdale Ss. (cf. Gaffney and Bartholomai, 1979), which is believed to be mid-Tertiary in age (Murphy et al., 1976). The similarity of this piece to the material from the Miocene Waite and Etadunna Fms. and the absence of similar material in the Plio-Pleistocene beds, suggests that the Oakdale Ss. may be Miocene in age.

TABLE 5: STRATIGRAPHIC RANGE OF CROCODILIANS IN THE QUEENSLAND CENOZOIC*

Holocene	*C. porosus*	*C. johnsoni*		
Pleistocene	*C. porosus*		*P. pollens*	
Pliocene	*C. porosus*		*P. pollens*	
Miocene				Murgon croc (?)

* Crocodilian material has also been reported from the probably Eocene Redbank Plains Fm by Reik (1952), see Molnar 1980) for comment.
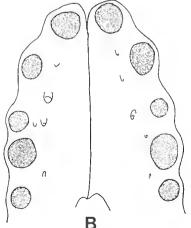
FIG. 8   Symphyseal regions, in outline, of the mandibles of *Pallimnarchus pollens* (A), and *Crocodylus porosus* (B). A based on QM F1149 (the lectotype), and B based on QM J29232. Not to scale.

DISCUSSION

Table 5 presents the temporal distribution of crocodilian taxa in Queensland from the Miocene to the present. It may be noted that there is no clear evidence of *C. johnsoni* in the fossil record: why this should be so for an endemic species is perplexing, although it seems likely that material simply has yet to be discovered. There is indication that *C. porosus* has inhabited Australia for several million years, at least since the early Pliocene (Molnar, 1979). Although *C. porosus* is now restricted to coastal rivers, during the Pliocene and Pleistocene it had apparently penetrated well inland. *P. pollens* appears to have been largely a crocodile of the inland waters.

Although *P. pollens* probably had a broader snout than *C. porosus*, there is no indication from jaw size that the skull was any larger than that of *C. porosus*. Hecht (1975) suggested that *P. pollens* had a heterodont dentition but there is no clear evidence for this assertion in any of the cranial material in the Queensland or Australian Museum collections. Indeed the teeth appear to have been generally similar to those of *C. porosus*, although some of the large isolated teeth attributed to *P. pollens* have regularly serrate carinae.

It seems likely that *Pallimnarchus* and *C. porosus* preyed upon the large marsupials of the Pliocene and Pleistocene, although doubtless feeding upon other forms as well.

CONCLUSIONS

Much material that has been attributed to *Pallimnarchus pollens*, at least in the Queensland Museum collections, cannot be certainly identified. Some of this material is not distinguishable from *C. porosus*. Some is clearly distinct from *C. prorsus* and is attributed to *P. pollens*. Longman's *C. nathani* cannot be distinguished from *C. porosus*, and thus is a junior subjective synonym of *C. porosus*. Both *P. pollens* and *C. porosus* material dates well into the Pliocene in age. Although now restricted to the coastal drainage, *C. porosus* penetrated well into the interior waters during the past. The large snout from Lansdowne, near Tambo, is attributed to *C. porosus* rather than *P. pollens*, on the basis of its proportions, external narial form, and dorsal sulci. Comparison of this snout with the *P. pollens* mandible from Macalister indicates that the snout of *P. pollens* must have been proportionately even broader than that of the Lansdowne specimen. There is no clear indication of *C. johnsoni* in the fossil record. A distinctive dentary piece from Murgon shows similarities to Miocene crocodilian material from South Australia and the Northern Territory, and suggests that the beds from which it derives (probably the Oakdale Ss.) may be Miocene.

LITERATURE CITED

DE VIS, C.W., 1886. On remains of an extinct saurian. *Proc. R. Soc. Qd*, **2**: 181–191.

———— 1907. Fossils from the Gulf Watershed. *Ann. Qd Mus.*, **7**: 3–7.

GAFFNEY, E.S. and A. BARTHOLOMAI, 1979. Fossil trionychids of Australia. *J. Paleont.*, **53**: 1354–60.

HECHT, M.K. 1975. The morphology and relationships of the largest known terrestrial lizard, *Megalania prisca* Owen, from the Pleistocene of Australia. *Proc. R. Soc. Vict.*, **87**: 239–50.

JACK, R.L. and R. ETHERIDGE, JR., 1892. 'The Geology and Palaeontology of Queensland and New Guinea'. 768 pp. (Brisbane: Govt. Printer).

LASERON, C.F., 1950. 'Ancient Australia'.

LONGMAN, H.A., 1924. Some Queensland fossil vertebrates. *Mem. Qd Mus.*, **8**: 16–25.

———— 1925. A crocodilian fossil from Lansdowne Station, *Mem. Qd Mus.*, **8**: 103–8.

———— 1926. A large jaw of *Pallimnarchus pollens*. *Mem. Qd Mus.*, **9**: 158–9.

MINCHAM, H., 1967. 'Vanished Giants of Australia'. (Adelaide: Rigby).

MOLNAR, R.E., 1979. *Crocodylus porosus* from the Pliocene Allingham Formation of north Queensland. Results of the Ray E. Lemley expeditions, part 5. *Mem. Qd Mus.*, **19**: 357–65.

———— 1980. Procoelous crocodile from Lower Cretaceous of Lightning Ridge, N.S.W. *Mem. Qd Mus.*, **20**: 65–76.

———— 1981. Pleistocene ziphodont crocodilians of Queensland. *Rec. Austral. Mus.*, **33**: 803–34.

MURPHY, P.R., et al., 1976. Geology of the Gympie 1: 250000 sheet area. *Rep. Geol. Surv. Qd*, **96**: 1–157.

RIEK, E.F., 1952. The fossil insects of the Tertiary Redbank Plains series. Part I: An outline of the fossil assemblage, with descriptions of the fossil insects of the orders Mecoptera and Neuroptera. *Univ. Qd Papers, Dept. Geol.,* **4**: 3–14.

STEEL, R., 1973. Crocodylia. In, Kuhn, O., ed. 'Encyclopedia of Paleoherpetology', vol. 16. 116 pp. (Stuttgart: Gustav Fisher Verlag).

WOODBURNE, M.O., 1967. The Alcoota Fauna, central Australia. *BMR Bull.,* **87.**

WOODS, J.T., 1960. Fossiliferous, fluviatile and cave deposits *J. Geol. Soc. Aust.,* **7**: 393–403.

PLATE 1

FIGS. A, B. Lectotype mandible (QM F1149) of *Pallimnarchus pollens* de Vis in ventral (A) and dorsal (B) aspects. Scale bar represents 2 cm here, all other scale bars represent 1 cm.

FIGS. C, D. Symphyseal platform of mandible (QM F11612) of *P. pollens* in ventral (C) and dorsal (D) aspects.

FIGS. E, F. Right side of symphyseal region of mandible (QM F11611) attributed to *Crocodylus porosus* in lateral (E) and dorsal (F) aspects. The symphyseal region here is narrower than in *P. pollens*. Note that this specimen is broken anteriorly at the level of the second alveolus, so that about 25% of the length of the symphysis is missing.

FIGS. G, H. Left quadrate (QM F1166) referred to *P. pollens* in ventral (G) and lateral (H) aspects. Anterior is to the left.
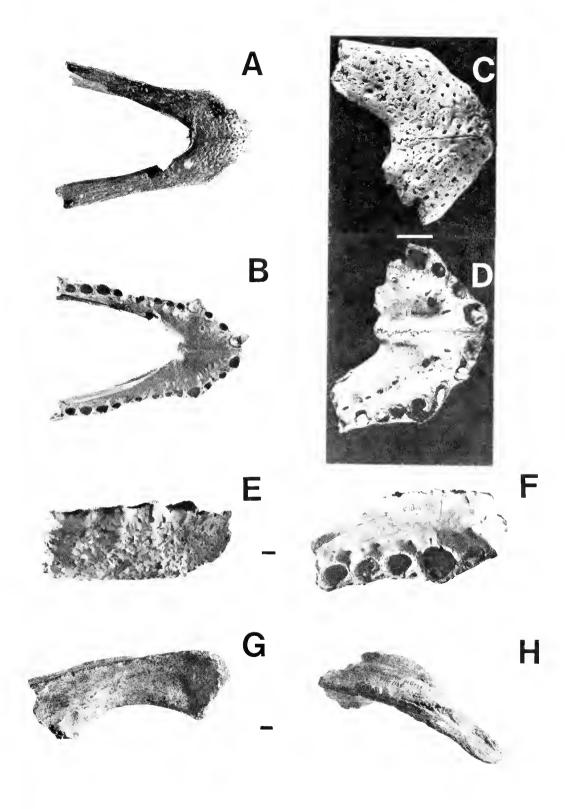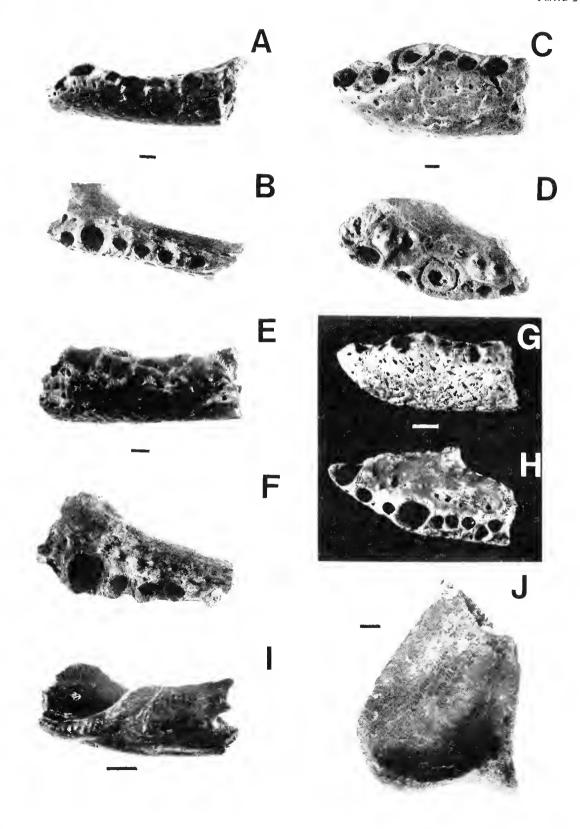
PLATE 2

FIGS. A, B. Lectotype mandible (QM F1513) of *Crocodylus nathani* Longman, in lateral (A) and dorsal (B) aspects. All scale bars represent 1 cm.

FIGS. C, D. Worn left symphyseal region of mandible (QM F1538) referred to *C. nathani* by Longman (124), but now recognized as *Pallimnarchus pollens*, in lateral (C) and dorsal (D) aspects.

FIGS. E, F. A second specimen (QM F1512) representing the same portion of the dentary as the lectotype from the hypodigm of *C. nathani* in lateral (E) and dorsal (F) aspects.

FIGS. G, H. Left symphyseal region (QM F11625) from possibly Miocene crocodilian in lateral (G) and dorsal (H) aspects. Specimen from near Murgon, southeast Queensland.

FIG. I. Incomplete left angular (QM F11610), associated in QM collections with lectotype mandible (QM F1149) of *Pallimnarchus pollens*, in medial aspect. Anterior is to the right.

FIG. J. Incomplete left quadrate (QM F1160) of *P. pollens* in ventral aspect. Anterior is to the top.

A LONGIROSTRINE CROCODILIAN FROM MURUA (WOODLARK), SOLOMON SEA

R.E. MOLNAR
Queensland Museum

ABSTRACT

Gavialis papuensis de Vis, represented by fragmentary remains of a mandible, vertebrae and dermal scutes, is not attributable to the genus *Gavialis*. The laterally directed mandibular alveolae, with projecting alveolar collars, suggest comparison with *Charactosuchus, Euthecodon* and *Ikanogavialis*. Similarity is greatest to the latter taxon. The specimen is too incomplete for confident definition, is probably of Pleistocene age and comes from Busai, Murua Island, in the Solomon Sea.

INTRODUCTION

De Vis (1905) described fragmentary crocodilian remains from Murua (Woodlark) Island, situated east of Papua New Guinea and ESE of the Trobriand Islands in the Solomon Sea (Fig. 1). He referred these remains to a new species, *Gavialis papuensis*, to my knowledge never again cited in the literature. The remains were attributed to a single individual and comprise two segments of the symphyseal region of the mandible with a single, incomplete tooth crown, now separated (QM F406), two cervical, one dorsal, one sacral and two caudal vertebrae (all

FIG. 1. World map showing localities of *Euthecodon* and crocodilians of similar habitus. A, *Charactosuchus kugleri*, Jamaica; B, *Ikanogavialis gameroi*, Venezuela; C, *C. fieldsi*, Columbia; D, *Euthecodon arambourgi*, Libya; E, *E. nitriae*, Egypt (Wadi Natron) and *E.* sp. Egypt (Moghara); F, *E. brumpti*, Ethiopia; G, *E.* sp., Kenya; and, H, the Murua crocodilian, Murua.

numbered QM F340), and one complete and one incomplete dorsal scute (both numbered QM F341).

The material is clearly not attributable to the genus *Gavialis* as it shows laterally projecting teeth and alveolar collars not found in that genus. These features are also found in *Charactosuchus, Euthecodon* and *Ikanogavialis*, all of which are found far from the Solomon Sea (Fig. 1). The absence of other narrow-snouted crocodilians from the New Guinea area makes it desirable to retrieve this material from obscurity (*Crocodylus novae-guineae*, although often described as narrow-snouted, is not really comparable to such forms as *Gavialis*, the dyrosaurs, or de Vis' material). This material is of further interest as it represents another occurrence of an unusual crocodilian habitus, probably later in date than most similar forms, and is the first to include postcranial material.

The abbreviation QM refers to the Queensland Museum.

LOCALITY AND STRATIGRAPHY

The fossils were collected from a mullock heap at Busai (de Vis, 1905). Trail (1967) shows Busai on Coleman's Ck., at the head of the Muniai River (Fig. 2). Three rock types are present at Busai: Tertiary intrusives, Okiduse Volcanics (Miocene), and Quaternary sediments. The fossils did not derive from the intrusives, but may have come from either of the other two units. The Okiduse Volcanics in this region consist of tuff, lava and agglomerate, and the Quaternary sediments include coralline limestone, clay, conglomerate and alluvium (Trail, 1967).

De Vis gives no information regarding the matrix found with the fossils, but a fine-grained bluish-grey matrix was present on one of the vertebrae. This matrix consisted largely of fragments of coralline limestone with a few quartz grains, so that the crocodilian remains likely derive from the Quaternary sediments.

DESCRIPTION

MANDIBLE. The two mandibular segments (Pl. 1) show no trace of the symphysis. There is no clear sign of contact between the two segment. One segment is preserved as a single piece, on one side (assumed to be dorsal) very slightly concave transversely, and on the other convex. Both surfaces bear short, shallow, narrow, longitudinal grooves, which are much more abundant on the convex surface. The alveoli face laterally and slightly dorsally, so that the long axis of each alveolus, projected into the transverse plane makes an angle of about 15 degrees with the horizontal. Most are empty, although roots or portions thereof are present in five. Where well-preserved the edges of the alveoli extend outward as low collars
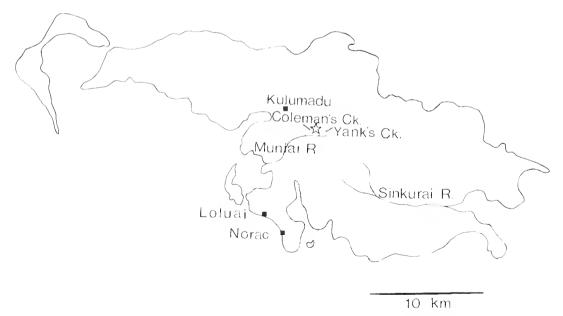
FIG. 2. Map of Murua (after Trail, 1967). Busai is represented by the star: the Murua crocodilian, *Chelone murua* and *Halicore brevirostre* were found in mine tailings in this area.

surrounding the aperture. Nowhere are these collars completely preserved. This segment bears remnants of eight alveoli per side.

The second segment is in two pieces, broken in the horizontal plane, but is otherwise much like the first. The pieces are less well-preserved showing much wear and some breakage. No alveolar collars are preserved, but the segment is so worn that none could be expected. No teeth are present, but each side of the segment bears evidence of eight alveoli. If both segments derive from the same individual, then it had at least fifteen alveoli on each side of the symphseal portion of the mandible.

TOOTH. A single, small, incomplete crown (Pl. 2, Figs. 6, 7) not mentioned by de Vis was found in the same specimen box as the mandibular segments and is thus assumed to pertain to this form. The crown is thin and recurved and fits none of the roots still in place. It bears distinct carinae, presumably anteriorly and posteriorly, and its surface is longitudinally striate.

CERVICALS. Two cervicals (Pl. 2,c), possibly successive, are preserved. Both are markedly procoelous with small, anteriorly placed hypapophyses. The neural arch is badly worn and lacks all processes on one and is missing from the other.

The parapophyses are low on the anterior half of the centrum, and the neural canal is roughly triangular in transverse section. In other features these cervicals are much like those of modern crocodilians.

DORSAL. A single dorsal (Pl. 2,d) resembles those of the existing Australian crocodilians, but with the anterior central face inclined at about 30 degrees to the long axis of the centrum. Of the neural arch only the left prezygapophysis remains, with the facet inclined at about 45 degrees to the horizontal.

SACRAL. The single sacral (Pl. 2,s) in addition to the centrum retains most of the arch but is lacking the postzygapophyses and the top of the neural spine. Both transverse processes are broken. The concave anterior central face is broad, and the convex posterior face is subtriangular in form with the apex ventral. The posterior face is set somewhat ventral to the anterior (as it is also on the dorsal centrum). The neural canal is subtriangular in section, and the prezygapophyseal facets are inclined to the horizontal at about 50 degrees. There are distinct sulci both anteriorly and posteriorly on the sacral ribs.

CAUDALS. One caudal (Pl. 2,k) lacking most of the arch, has a double keel ventrally terminating both anteriorly and posteriorly in facets for the chevrons. The posterior central face is set lower than the anterior, but not by as great a degree as in the dorsal and sacral. The second centrum (Pl. 2,k) with the arch disarticulated is unusual and may not be a caudal. The concave lateral and ventral surfaces of the centrum meet in a long process, now broken. Such processes are not found on any of the other crocodilian material available to me for reference, and do not have the appearance of pathological features.

SCUTES. The osteoscutes (Pl. 2, Figs. 4, 5; de Vis, 1905, pl. 13) need no detailed description. Both scutes are bevelled along one margin, and bear a sutural articular surface along an adjacent margin (Pl. 2, Fig. 4)

COMPARISON.

The long, narrow symphyseal region restricts comparison to longirostrine forms, and in view of the recent date only Cenozoic forms will be considered. These include: *Characiosuchus*, *Crocodylus (cataphractus* and *johnsoni)*, *Dollosuchus*, *Dyrosaurus*, *Eosuchus*, *Euthecodon*, *Gavialis*, *Gavialosuchus*, *Hesperogavialis*, *Hyposaurus*, *Ikanogavialis*, *Phosphatosaurus*, *Rhabdognathus*, *Rhamphostomopsis*, *Rhamphosuchus*, *Tilemsisuchus* and *Tomistoma*. Of these, most have the mandibular alveoli orientated vertically unlike the Murua form: this leaves only *Characiosuchus*, *Ikanogavialis* and *Euthecodon* for close comparison (Fig. 3).

Characiosuchus is represented by *C. fieldsi* (Langston, 1965) from the late Miocene of Colombia and *C. kugleri* (Berg, 1969) from the Eocene of Jamaica, and *Ikanogavialis* (Sill, 1970) by the single species *I. gameroi* from the late Miocene (Bocquentin Villanueva & Buffetaut, 1981) of Venezuela. *Euthecodon* is represented by three species. The earliest and least developed is *E. arambourgi* (Ginsburg and Buffetaut, 1978) from the Burdigalian of Libya and Egypt. *E. nitriae* (Fourtau, 1920) ranges from the Burdigalian to the Villafranchian in Egypt (Ginsburg & Buffetaut, 1978), and the most extreme, *E. brumpti* (Joleaud, 1920) comes from the Villafranchian of Ethiopia. *Euthecodon* sp. has also been found in the early Miocene of Kenya (Buffetaut, 1979; Ginsburg & Buffetaut, 1978; Tchernov & Van Couvering, 1978) and the Pleistocene of Ethiopia (Arambourg, 1948). Murua is over 10,000 km from Ethiopia and farther from the other mentioned localities, and if

the stratigraphy of the Murua deposits is correctly interpreted, the Murua crocodilian is younger than *C. kugleri*, *C. fieldsi*, *I. gameroi* and *E. arambourgi*, and quite possibly younger than *E. nitriae* and *E. brumpti* as well.

Little or no mandibular material has been figured for either *E. nitriae* or *E. arambourgi* so comparison cannot be made. The relatively broad (for a *Euthecodon*), tapered snout of *E. arambourgi* (Fig. 3) suggests that the mandibles might also have been tapered and hence unlike those from Murua which show no evidence of taper. The Murua mandibular pieces show no symphyseal suture unlike the figured specimens of most other forms. The figured material of *E. brumpti* (Arambourg, 1947) however shows little indication of the symphyseal suture. All of the *Euthecodon* mandibles (especially those from the Miocene) appear to differ from that of the Murua crocodilian by their longer alveolar collars. Since all of the collars of the Murua material are both broken and worn some doubt must remain about this distinction.

If the *G. papuenis* mandibular fragments pertain to a single individual it would have at least fifteen alveoli per side. *C. fieldsi* has only ten per side along the symphyseal rostrum and *C. kugleri* nine, while *E. brumpti* and *I. gameroi* both have more than fifteen alveoli per side and thus more closely approach *G. papuensis*. A further point of similarity with *I. gameroi* lies in the proportions of the mandibular pieces.

These longirostrine crocodilians with alveolar collars may be divided into two groups on the ratio of the breadth of the symphyseal portion of the mandibles (taken between the alveolar collars) to the average alveolar diameter. In both *Charactosuchus* and *Euthecodon* (except *E. arambourgi* which has a tapered snout) this ratio is approximately two, while in *G. papuensis* and *I. gameroi* it is approximately three. This ratio provides a measure of the apparent width of the symphyseal portion of the mandibles.

Arambourg (1947, pl. 35, fig. 5) figured a single crown of *E. brumpti*, which while generally similar to that of the Murua crocodilian, is broader in silhouette distally.
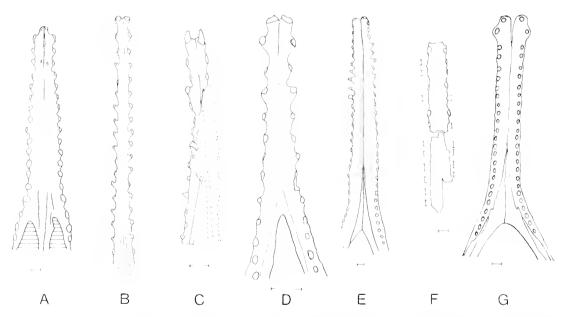
FIG. 3. Mandibular rostra (and one snout) of longirostrine crocodilians with alveolar collars. A, *Euthecodon arambourgi* (snout); B, *Euthecodon brumpti*; C, *Charactosuchus fieldsi*; D, *Charactosuchus kugleri*; E, *Ikanogavialis gameroi*; F, the Murua crocodilian, (the bracketed bars indicate alveoli not obvious in the outline); and G, *Gavialis gangeticus*. A in ventral view, all others in dorsal view, scale bars represent 2 cm, scale for B not available. The different orientation of the alveoli and absence of alveolar collars in *Gavialis* is apparent (the collars are broken on the Murua material).

DISCUSSION

Langston (1965, p. 40) has commented that 'Longirostrine crocodilian mandibles are even more difficult to distinguish systematically than are the skulls'. Thus no firm identification is attempted here, especially in view of the incomplete nature of the Murua material, and of the absence of descriptions of postcranial material of the comparable described taxa. Because of this the postcranial material referred to *G. papuensis* does not reveal sufficiently distinctive character states to allow adequate diagnosis at this time. The mandibular material may be distinguished from *Euthecodon* and *Charactosuchus*, but not confidently from *Ikangavialis*. *G. papuensis* is not attributable to *Gavialis* and thus may be designated *"Gavialis" papuensis*. This is not a satisfactory designation, but pending discovery of further material it seems best to defer formal taxonomic action.

With regard to the phyletic relations of the Murua crocodilian there is only the single character state (ratio of alveolar diameter to width of mandible between alveoli) shared with *Ikanogavialis*. This may indicate a phyletic relationship with *I. gameroi*, but in the absence of supporting evidence especially regarding variability of this state this is a hypothesis not a conclusion.

Its occurence in the Solomon Sea would represent a considerable extension of range were the Murua form related to either South American forms or *Euthecodon*. In any event it shows that this particular, sawfish-like habitus was more widespread than previously believed.

The material of the Murua crocodilian was apparently found with the remains of two other vertebrates, the marine turtle *Chelone murua* and the dugong *Halicore brevirostre* (de Vis 1905). Both of these suggest a marine, or at least lagoonal environment, and suggest that the Murua crocodilian may have been a marine form. Thus the resemblance of the symphyseal region of the mandible to the rostrum of a sawfish especially in tooth orientation may reflect some similarity of environment and habits.

ACKNOWLEDGEMENTS

LITERATURE CITED

ARAMBOURG, C. 1948. Mission scientifique de l'Omo (1932–1933). t. **1** (3), Paléontologie. (Paris: Edit. Mus.)

BERG, D.E. 1969. *Charactosuchus kugleri,* eine neue Krokodilart aus dem Eozän von Jamaica, *Eclog. Geol. Helvet.,* **62**, 2: 731–5.

BUFFETAUT, E. 1979. Présence du Crocodilien *Euthecodon* dans le Miocène inférieur d'Ombo (Golfe de Kavirondo, Kenya). *Bull. Soc. Géol. France,* (7), **21**, 3: 321–2.

FORTAU, R. 1918. Contribution à l'etude des vertébrés miocènes de l'Egypte. *Geol. Surv. Egypt,* **1918**: 1–99. (not seen).

GINSBURG, L., & E. BUFFETAUT. 1978. *Euthecodon arambourgi* n. sp., et l'évolution du genre *Euthecodon,* crocodilien du Néogène d'Afrique. *Geol. Med.,* **5**: 291–302.

JOLEAUD, L. 1920. Sur la présence d'un Gavialidé du genre *Tomistoma* dans le Pliocène d'eau douce de l'Ethiope. *C.R. Acad. Sci.,* **170**: 816–8.

LANGSTON, W., JR. 1965. Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America. *Univ. California Publ. Geol. Sci.,* **52**: 1–157.

SILL, W.D. 1970. Nota preliminar sobre un nuevo gavial del Plioceno de Venezuela y una discusion de los gaviales sudamericanos. *Ameghiniana,* **7**: 151–9.

STEEL, R. 1973. Crocodylia. In, Kuhn, O., ed. 'Encyclopedia of Palaeoherpetology', vol. 16. 116 pp. (Stuttgart:Gustav Fisher Verlag).

TCHERNOV, E., & J. VAN COUVERING, 1978. New crocodiles from the early Miocene of Kenya. *Palaeontology,* **21**, 857–67.

TRAIL, D.S. 1967. Geology of Woodlark Island, Papua. *BMR Rept.,* **115**: 1–32.

DE VIS, C.W. 1905. Fossil vertebrates from New Guinea. *Ann. Qd Mus.,* **6**: 26–31.

NOTE ADDED IN PROOF

Fossil material from Murua was donated to the Australian Museum in 1899 (Etheridge, 1900: 7, also 24). This consisted of dorsals doubtfully attributed to *Crocodylus porosus* and vertebrae attributed to *Halicore dugong*, from 'the Gold-bearing drift': no further details were published. A recent search for this material and a relevant letter turned up only the dugong material (AM F5795), however the other specimens may yet be rediscovered. Whether this is the specimen mentioned by Stanley (1912:9) as uncovered 'In the black silt' near Busai cannot be determined. Murua is well within the range of *C. porosus* today. Mrs D. Jones and Dr A. Ritchie kindly sought the material and letter and Ms T. Lees thoughtfully drew my attention to these reports.

ETHERIDGE , R., Jr., 1900. Curator's report for 1899. *Austral. Mus. (Rept. Trustees)*, **1899**: 3–7. (Appendix 1.)
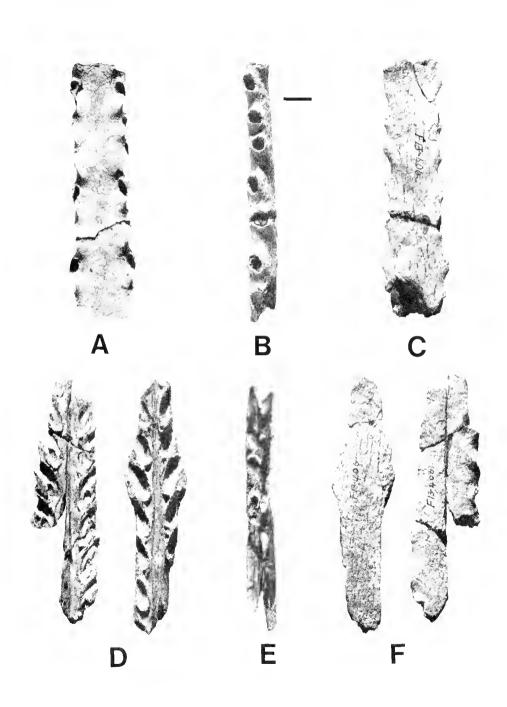
STANLEY, E.R., 1912. Report on the geology of Woodlark Island. *Comm. Austral. Rept. Terr. Papua*, **1911-1912**: 1–23.

PLATE 1

The two mandibular segments of the Murua crocodilian (QM F406). First segment in dorsal (A), lateral (B), and ventral (C) aspects. The two portions of the second segment in internal (D) and external (F) aspects: in the latter on the left is the presumed ventral piece and on the right the presumed dorsal. E shows the two pieces together in lateral view. Scale bar represents 2 cm.

A   B   C

D   E   F
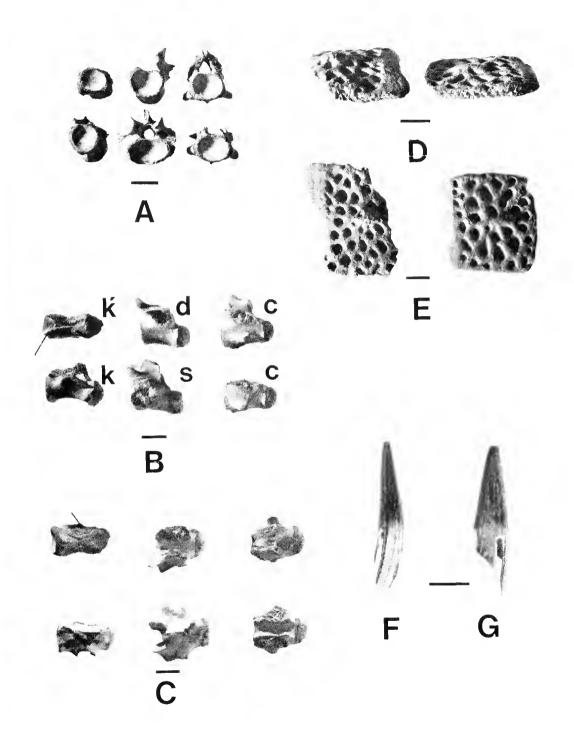
PLATE 2

Further material attributed to the Murua crocodilian. Vertebrae (QM F340) in anterior (A), left lateral (B), and dorsal (C) aspects. In each the scale bar represents 2 cm, and the arrangement (indicated in B) is: c, cervicals; d, dorsal; s, sacral; k, caudal, and; k', presumed caudal. The ventrolateral process of the presumed caudal, discussed in the text, is indicated by the inclined lines. Dorsal scutes (QM F341) in oblique (D) and dorsal (E) aspects. The sutural surfaces are seen in D. Scale bars represent 1 cm.

Tooth presumably associated with mandibular segments in anterior or posterior aspect (F) and medial aspect (G). Scale bar represents 0·5 cm.

PLEISTOCENE RECORDS OF *FALCO BERIGORA* FROM AUSTRALIA AND THE IDENTITY OF *ASTURAETUS FURCILLATUS* DE VIS (AVES:FALCONIDAE)

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ABSTRACT

Restudy of the fossil falconiform material described by C.W. de Vis has shown that only *Asturaetus furcillatus* from the Pleistocene of Cooper Creek, northeastern South Australia, belongs to the Falconidae. It, and another fossil from the Pleistocene of Lake Menindee, western New South Wales, are here referred to the living species *Falco berigora*.

INTRODUCTION

During the late 19th and early 20th centuries, C.W. de Vis (1890, 1891, 1892, 1905) described several fossil raptors as members of the Falconidae including: *Uroaetus brachialis, Necraster alacer, Taphaetus lacertosus, Asturaetus furcillatus,* and *Baza gracilis.* At that time the Falconidae included the Accipitridae (Sharpe 1874), now a separate family. Within the present family Falconidae are four subfamilies: Herpetotherinae, Polyborinae, Falconinae, and Polihieracinae (Peters 1931). Most of the fossils de Vis originally assigned to the Falconidae were later referred to the Accipitridae. Only one, *Asturaetus furcillatus,* from Pleistocene sediments along Cooper Creek, South Australia, is now regarded as being a falcon (Brodkorb, 1964). Our examination of the type reveals that both this and a tibiotarsus discovered since the work of de Vis in Pleistocene sediments at Lake Menindee, New South Wales, are referable to the living species of *Falco berigora.*

Abbreviations: ANWC, Australian National Wildlife Collection, CSIRO, Division of Wildlife Research, Canberra; NMV, National Museum of Victoria, Melbourne; QM, Queensland Museum, Brisbane; UCMP, University of California, Museum of Paleontology, Berkeley; and USNM, United States National Museum of Natural History, Washington, D.C.

Falco berigora Vigors and Horsfield 1827

THE DE VIS MATERIAL: *Asturaetus furcillatus* de Vis, 1905.

Holotype, a nearly complete right tibiotarsus, lacking parts of proximal end, QM F5509 (see Pl. 1), from Pleistocene-aged deposits along the lower Cooper Creek, northeastern South Australia, Lake Eyre Basin.

COMMENT AND DIAGNOSIS

In recording the Pleistocene collections of J.W. Gregory from the Lake Eyre Basin, South Australia, de Vis (1905) described *Asturaetus furcillatus* as a hawk, intermediate between a goshawk *(Accipiter = Astur)* and the litte eagle *(Hieraaetus = Nisaetus).* After consulting de Vis and using a name suggested by de Vis, Richmond (1909) substituted *Plioaetus* for *Asturaetus* de Vis which is preoccupied by *Asturaëtos* Brehm 1855. Richmond, with a query, referred *P. furcillatus* to the Buteonidae, in which he included goshawks and eagles. Brodkorb (1964) and Condon (1968) placed *P. furcillatus* with the falcons in the Falconidae, but later Condon (1975) placed it with the goshawks in the Accipitrinae. We found that the type, which is the only published material of *Plioaetus furcillatus,* belongs within the extant genus *Falco,* and furthermore to the living species *F. berigora.*
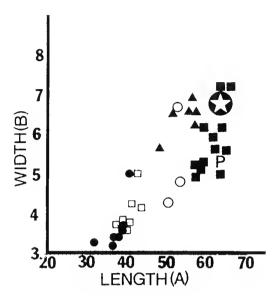
FIG 1. Plot of tibiotarsal proportions of fossil and recent falcons from Australia. Length (mm) = length of tibiotarsus from distal end of fibular crest to distal end of bone (A of Table 1), and width = width of shaft at base of fibular crest (B) ● = *Falco cenchroides;* □ = *F. longipennis;* o = *F. subniger;* ■ = *F. berigora;* ▲ = *F. peregrinus;* * = the Menindee *F.* rf *berigora;* and P = *Asturaetus (Pliotaetus).*
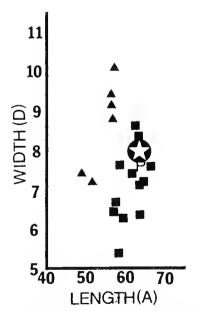
In our sample of ten modern *F. berigora* (see Pl. 1, Tab. 1, and Figs. 1 & 2), we found sufficient variability in the tibiotarsi to encompass the character-states de Vis believed diagnostic for *P. furcillatus:* (1) the presence of a distinct, shallow groove between the outer edge of the shaft and the supratendinal bridge (= 'bridge for the extensor tendon') and (2) the greater dilation of the internal border of the shaft distally. A third character that de Vis believed to be 'the most peculiar feature of this tibia' is the Y–shaped nature of the supratendinal bridge producing three distal openings which, however, is actually a diagnostic feature of *Falco* and most of the rest of the Falconidae.

P. furcillatus can, furthermore, be distinguished from members of subfamilies of Falconidae other than the Falconinae in the same manner as the falcon from Lake Menindee discussed later in this paper. Thus on the basis of similarity of size and morphology to the extant *Falco berigora*, we consider *Plioaetus* Richmond 1909 to be a junior synonym of *Falco* Linneaus 1758 and *Asturaetus furcillatus* de Vis 1905 to be a junior synonym of *Falco berigora* Vigors and Horsfield 1827.

FIG 2. Plot of tibiotarsal proportions of fossil and recent falcons from Australia. For length see Fig. 1; Width = width of shaft at proximal end of supratendinal bridge. See Fig. 1 for legend.

THE MENINDEE MATERIAL

A partial right tibiotarsus, UCMP 79276, (Pl. 1 and Figs. 1 & 2, Tab. 1), was recovered from UCMP Loc. V-67185, (= UCMP V5371, Lake Menindee 2), a blowout in the sand hills along the northwestern shore of Lake Menindee, south of Broken Hill, western New South Wales. This and several other sites in near proximity have yielded a rich collection of vertebrates (Tedford 1967), including birds. One specimen was the tibiotarsus of a large falcon. The Menindee falconid was recovered from the basal part of the exposed lunette sequence from which *Diprotodon* was also obtained. In an adjacent site, Site 1, 1600 yards (1·5 km) west of Site 2 (University of California, Museum of Paleontology localities) on the south-western horn of the lunette, the mammal fauna from the basal part of the exposed section included *Thylacinus, Sarcophilus, Procoptodon, Sthenurus,* and *Macropus* (presumably contemporaneous with the fossil falconid). This fauna roughly correlates (R.H. Tedford, pers. comm., 1976) with that from the older lunette of Lake Menindee (see Tedford 1967) and indicates a late Pleistocene age.

DIAGNOSIS

Although every genus in the family Falconidae was not available for comparison, tibiotarsi of *Herpetotheres (H. cachinnans,* USNM 491335), *Polyborus (P. plancus,* USNM 428041), and *Polihierax (P. semitorquatus,* USNM 322394), as well as those of several species of *Falco* (including all Recent Australian species) were compared with the fossil. Such a collection represents each of the four subfamilies of the Falconidae recognized in Peters (1931) (Herpetotherinae, Polyborinae, Falconinae, and Polihieracinae), and even though the latest revision of the Falconidae (Brown and Amadon 1968) does not recognize formal subfamilial groupings, the above genera clearly represent the breadth of variation within the family. The Menindee falconiform tibiotarsus is assigned to the Falconidae because the tendinal canal on the distal end of the bone has three openings, characteristic of this family alone. The tibiotarsus most closely resembles those of the genus *Falco* (Falconinae) and differs from those of other subgroups within the Falconidae as follows:

HERPETOTHERES (HERPETOTHERINAE)

The Menindee specimen differs in that it lacks a tendinal groove demarked by a distinct ridge on either side of lateral shaft surface near distal end; has the distolateral opening of tendinal canal as large or nearly as large as other two openings in same area; the long axes of medial and lateral flanges of the supratendinal bridge form small acute angles with long axis of the shaft; in posterior view, the lateral surface of the shaft near the distal end is 'dished out', concave posterolaterally.

POLYBORUS (POLYBORINAE)

The Menindee specimen differs in that the lateral border of the proximal opening for the tendinal canal protrudes farther anteriorly than does the medial border; the proximal opening of the tendinal canal does not exceed half of the shaft width; the distolateral opening of the tendinal canal is nearly as large or as large as the other two openings; the external condyle does not extend beyond the lateral margin just proximal to this condyle.

TABLE 1: MEASUREMENTS IN MILLIMETRES OF THE TIBIOTARSI OF FOSSIL AND RECENT AUSTRALIAN FALCONIDAE

	Falco hypoleucus ANWC (x-ray photograph)	*Falco berigora* (UCMP 79276)	*Asturaetus (=Plioaetus) furcillatus* (QMF5509)	*Falco berigora* (n = 14)	*Falco peregrinus* (n = 6)	*Falco cenchroides* (n = 7)	*Falco longipennis* (n = 7)	*Falco subniger* (n = 3)
A. Length from distal end of fibular crest to distal end of tibiotarsus.	51·8	64·6	64·2	57·5–66·6	48·7–57·8	31·6–40·1	39·4–43·3	50·2–53·8
B. Width of shaft at distal end of fibular crest.	5·2	6·8	5·8	5·0–7·2	6·2–6·9	3·2–5·0	3·6–5·0	4·3–6·7
C. Maximum depth of shaft at distal end of fibular crest.	—	5·6	5·6	4·3–5·8	5·0–6·2	2·9–3·5	3·2–4·1	3·8–4·8
D. Width of shaft at proximal end of supratendinal bridge.	—	7·6	8·8	6·3–8·8	7·4–10·1	3·6–4·8	4·3–5·7	6·7–7·9
E. Depth of shaft at proximal end of supratendinal bridge.	—	5·6	4·7	4·0–5·6	5·1–5·6	2·4–3·3	2·9–3·8	3·8–5·0
F. Length of external condyle, viewed anteriorly.	6·2	6·2	6·6	5·4–6·6	5·8–7·4	3·1–3·9	3·4–4·0	5·9–6·1
G. Maximum width distal end	12·4	—	11·5	9·7–11·5	11·6–14·4	6·4–7·2	6·7–8·4	11·0–11·7
H. Depth internal condyle.	8·7	—	7·9	7·4–9·1	8·3–9·7	4·8–5·6	4·9–5·9	7·3–8·0
I. Depth external condyle.	—	—	8·1	7·3–8·9	7·7–9·9	4·8–5·4	5·0–5·7	7·6–7·9
J. Length of fibular crest.	15·0	—	@14·6	11·6–17·4	18·0–18·9	8·5–11·2	8·4–10·9	11·4–13·6

POLIHIERAX (POLIHIERACINAE)

The Menindee specimen differs in that the proximal opening for the tendinal canal tends to be situated near the midline of shaft or slightly medial to it rather than lateral; a broad shelf of bone lies lateral to the distolateral opening of the tendinal canal; in posterior view, the lateral surface near the distal end is 'dished out' rather than being convex posterolaterally.

Against this background of comparison, the Menindee tibiotarsus has been assigned to the genus *Falco*.

COMMENTS

Figs. 1 and 2 and Tab. 1 illustrate how the Menindee specimen is similar in size to specimens of *Falco peregrinus* and *F. berigora,* and larger than specimens of the other Australian falcons, *F. hypoleucos, F. cenchroides, F. longipennis,* and *F. subniger.*

Even though qualitative characters can be quite variable within any one species of living falcon, a few appear to show consistent differences between some of the Australian falcons and the Menindee specimen. In lateral view, the posterior margin of the shaft is very straight in the Menindee specimen, but distinctly concave in *F. subniger* and *F. longipennis.* In the Menindee specimen, the anterior surface of the shaft is only slightly convex, whereas in most specimens of other Australian falcons this area is more highly arched, but both flattened and arched conditions were observed in *F. berigora.*

Based on the above comparisons, the match of the Menindee specimen is close enough to the tibiotarsi of the living Brown Falcon, *F. berigora* to be assigned to it. Although the tibiotarsi of *F. peregrinus* is also quite similar to both the Menindee specimen and de Vis' *Asturaetus,* it differs in being more robust, while the two fossils and the tibiotarsi of *F. berigora* are more gracile.

LITERATURE CITED

BRODKORB, P., 1964. Catalogue of fossil birds, Part 2. *Bull. Florida State Mus.* **8** (3): 291.

BROWN, L. & D. AMADON, 1968. Eagles, Hawks, and Falcons of the World.' (New York: McGraw-Hill.)

CONDON, H.T., 1968. 'A handlist of the birds of South Australia.' 2nd ed. (Adelaide: S. Aust. Ornith. Assn.) 141 pp.

    1975. 'Checklist of the birds of Australia, Part 1. Non-passerines.' (Melbourne: RAOU.)

DE VIS, C.W., 1890 (1889). On a bone of an extinct eagle. *Proc. Roy. Soc. Qd* **6:** 161–2.

    1891. Note on an extinct eagle. *Proc. Linn. Soc. N.S.W.* **2** (6): 123–5.

    1892. Residue of the extinct birds of Queensland as yet detected. *Proc. Linn. Soc. N.S.W.* **2:** 437–56.

    1905. A contribution to the knowledge of the extinct avifauna of Australia. *Ann. Qd Mus.* **6:** 3–25.

LINNAEUS, C., 1758. 'Systema naturae.' 10th ed. (Stockholm) **1:** 824 p.

PETERS, J.L., 1931 'Check-list of Birds of the World.' 1. (Cambridge, Mass.: Harvard Univ. Press) 1–345 + xviii.

RICHMOND, C.W., 1909 (1908). Generic names applied to birds during the years 1901 to 1905, inclusive, with further additions to Waterhouse's 'Index Generum Avium.' *Proc. U.S. Nat. Mus.* **35** (1656): 583–655.

SHARPE, R.B., 1874. 'Cat. Birds Brit. Mus.' **1:** 479 pp.

TEDFORD, R.H., 1967. The fossil Macropodidae from Lake Menindee, New South Wales. *Univ. California, Publ. Geol. Sci.* **64:** 156 pp.

VIGORS, N.A. & T. Horsfield, 1827. A description of the Australian birds in the collection of the Linnean Society. *Trans. Linn. Soc. London.* **15:** 170–331.

PLATE 1. Anterior views of tibiotarsi of:
(A) *Falco berigora* (Modern, Australia),
(B) *Asturaetus (=Plioaetus) furcillatus* (Pleistocene, Lower Cooper Creek, S.A. QM F5509), and (C) *Falco* rf. *berigora* (Pleistocene, Lake Tandou, N.S.W., UCMP 79276).

a.   b.   c.

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